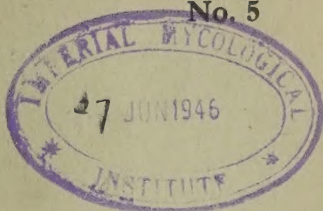


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E. H. FULLING

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CYTOLOGY OF CEREALS. II*

HANNAH C. AASE

State College of Washington

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INTRODUCTION

The first decade, freely speaking, of intensive work in the cytology of "small grain" cereals (1), and closely related grasses, may be characterized mainly by determination of chromosome numbers in supposedly well established races and species, and by description of general chromosome behavior in a number of varietal, specific and

* Supplement to article in *The Botanical Review* 1: 467-496. 1935.

generic hybrids. The second, or immediately past, decade, and the sundry burden of this review, has become progressively more marked by increased artificial induction of disturbances of the apparently stable state of nature, or perhaps, more exactly speaking, by attempts to speed up processes of slowly rolling spontaneous evolution. A rugged stability on one hand is yet highly susceptible to change which often manifests itself cytologically as chromosome aberrations, numerical and structural.

EUPLOID CHROMOSOME ABERRATIONS

Spontaneous Autoploid Aberrations

The occurrence in plant species of natural races with unlike chromosome numbers is no longer considered rare. Temporary confusion, sometimes resulting from diverse taxonomic interpretations, demands permanent recorded data and ample plant specimens to assure the future validity of the respective cytological research. These precautions will become even more imperative as the number of autoploid and allopolyploid aberrants are multiplied. Avoidance of further confusion in nomenclature merits a close cooperation of both cyto-geneticists and taxonomists in naming newly obtained aberrants, spontaneous or induced, that may become destined to exist as permanent species.

The evidence for spontaneous euploid duplication or reduction may seem fairly conclusive to quite obscure. Müntzing (343) has appropriately stated that all allopolyploids are partially autoploid. Most of the forms of the newly discovered Georgian wheat species, *Triticum Macha* Dek. et Men. (330), possessed the somatic chromosome number 42, but a small group had the number 28. Morphologically the hexaploids and tetraploids were almost identical. The tetraploids were thought to have arisen from the hexaploids by mutation, and have been designated as *Triticum dicoccum* ssp. *georgicum* Dek. et Men. Tumanian (534) found in the progeny of a wild diploid wheat, in addition to tetraploid individuals, a tetraploid head on a diploid plant. The mutant head generally, though not completely, resembled in enlarged dimensions the original form, and was named *Triticum Jerevani*. Robertson and Weaver (433) found a giant, apparently tetraploid, form of *Agropyron spicatum* growing adjacent to the normal diploid.

When races of unlike euploidy in a species occur in diverse geo-

graphical regions, the specific bond is assumed usually on the strength of morphological likeness. *Agropyron junceum* occurs as a tetraploid along the Atlantic shores from Portugal to Scandinavia, and is present as a more robust hexaploid along the shores of the Mediterranean (385). *Agropyron cristatum* comprises diploid, tetraploid and hexaploid races (32); *A. intermedium*, tetraploid (209) and hexaploid (32, 209); *Hordeum nodosum*, diploid and tetraploid (82, 510); and *H. murinum*, diploid (393, 528) and tetraploid (30, 82, 529). Summaries of chromosome numbers (528, 530) will reveal yet other species, including races or subspecies, with dissimilar euploidy.

Decrease in euploidy is most commonly observed in the form of haploidy. Haploids arise spontaneously in plant populations at frequencies apparently determined by species, race and ecological conditions. Raw (429) attributed the 0.0001% frequency of haploids in *Triticum vulgare* to excessively high temperature at time of flowering. Yamasaki (571) found a frequency of 0.029% of wheat haploids among 33,600 non-hybrids, and 0.025% among 211,600 hybrids. Volunteer haploids have been found also in *T. monococcum* (495), *T. spelta* (484) and *Secale cereale* (285).

One source of spontaneous euploid chromosome aberrants is polyembryony. Yamamoto (570) has found that the incidence of polyembryony is variable with plant, strain or hybrid, and he is, no doubt, justified in assuming that twinning is genetically conditioned. Tabulated reports by Müntzing (346) corroborate this assumption; e.g., the "Stålråg" variety of rye produced a much higher proportion of multiple embryos than the "Kungsråg". An approximate summary of available counts of multiple embryos in cereals, including *Triticum* (257, 346, 568, 569), *Secale cereale* (257, 346, 460), *Hordeum vulgare* (346) and *Avena sativa* (346), reveals that 2,186,486 caryopses produced 764 sets of twins, seven sets of triplets and one set of quadruplets, or, briefly, one set of multiple embryos per 2,832 grains. In *T. monococcum* twin embryos occurred only after cross pollination, and with increased frequency following delay in pollination (221), attaining under the latter conditions a high frequency of three pairs of twins among 195 seedlings.

Table 1, based on most of the compilable data (213, 257, 346, 347, 460, 568, 569), shows that polyembryony in cereals is a poor source

TABLE 1
RATE OF OCCURRENCE OF ABERRANT CHROMOSOME NUMBERS
AMONG MULTIPLE EMBRYOS

Plant species and 2n chromosome No.	No. of caryopses	No. of embryos and degree of euploidy		
		$\frac{1}{2} \times 2n$	$1\frac{1}{2} \times 2n$	$2 \times 2n$
<i>Triticum vulgare</i> (42)	246	4 (21)	23 (63)	0
<i>T. durum</i> (28)	8	1 (14)	0	0
<i>T. turgidum</i> (28)	3	0	2 (35)	0
<i>Secale cereale</i> (14) ...	799	2 (7)	2 (21)	1 (28)
<i>Hordeum vulgare</i> (14)	47	2 (7)	1 (21)	0
<i>Avena sativa</i> (42)	131	0	23 (63)	1 (84)
Total	1234*	9	51	2

* Includes six sets of triplets and one set of quadruplets, occurring mainly in *Secale*.

of "tetraploids"¹, a fair source of haploids and a comparatively rich source of "triploids". Among 1,234 polyembryonal caryopses, approximately 60 produced a pair of twins with unlike chromosome numbers. A *Triticum vulgare* triplet produced two "triploids" and one normal (569).

The origin of multiple embryos, in general, has been fully discussed by Webber (566). The source of the second member of a "diploid" pair of twins has been attributed to post-fertilization cleavage (419) and to antipodal fertilization (257); the "triploid" member of a "diploid-triploid" pair to embryonal development of a fertilized endosperm cell (257, 569) and to a fertilized unreduced nucleus of a supernumerary embryo sac (346); and the haploid member of the less frequently occurring haploid-"diploid" combination to parthenogenesis of the reduced egg cell (221, 569). The fortunate finding of twins in F_1 hybrids, as reported by Kasparyan (190), reveals more definitely to what extent the ♂ elements participated in the formation of the embryo. In a varietal tetraploid wheat cross, one twin was a normal "diploid" hybrid, the other a haploid replica of the ♀ parent and must have sprung apomictically from an extra egg cell, antipodal or synergid. A hexaploid-tetraploid wheat cross proved even more instructive in that one twin was a hybrid with the expected three genomes from the ♀ and two genomes from the ♂; the second twin also was a hybrid with three genomes from

¹ Tetraploid, triploid, etc., in quotation marks are used in the loose sense in this review to signify $2 \times$ and $1\frac{1}{2} \times$ somatic number, respectively, and may or may not correspond to the number of genomes.

the ♀ but apparently with four genomes from the ♂, indicating, perhaps, that one pair of sperms fertilized the egg and endosperm, and a second pair fertilized an extra egg cell, a synergid, or an antipodal.

Outside the category of polyembryony the exact causes of spontaneous euploid chromosome changes are equally obscure. Some are no doubt the result of mitotic aberrations in vegetative tissue in a cell line leading to sex cells (285), and may include larger portions of the plant, demonstrated by various forms of chimera (357, 534), or may be discovered as small blocks of aberrant cells in reproductive tissue, as entire locules, or parts of locules of anthers (78, 276, 344, 577). Large spore mother cells, with multiplied euploidy, either singly or in smaller or larger groups, are not an unfamiliar sight in routine studies of anther material. An extreme case of multiploid sporocytes was observed in *Hordeum vulgare* (502). As hybrid material is perhaps more intensively studied and also more unstable, reports (107, 110, 224) have been more numerous from this source. Drought (224) and high temperature (177) are apparently conducive to development of these large cells.

Haploid cells in unreduced tissue in a "diploid" plant are rare. Haploid pollen mother cells were, however, observed in a 42-chromosome segregate of a pentaploid wheat cross (296).

Induced Autoploid Aberrations

"Tetraploids" have developed after treatment with colchicine in wheat (100, 392), rye (57, 85, 461), barley (78, 100, 145, 188) and oats (100, 461); after exposure to X-rays in rye (56); and after exposure to high temperatures in wheat (99), rye (99) and barley (121, 185, 186, 358).

One triploid plant of *T. monococcum* was obtained after pollination with X-rayed pollen (230). Also one triploid and one short-lived octoploid were obtained in rye through colchicine treatment (57).

Haploids have arisen in rye following exposure to high (375) and low (345) temperatures. Emasculation with subsequently attempted hybridization has resulted in haploids in wheat (362, 495, 557), and in conjunction with colchicine in *Aegilops ovata* (325). Emasculation by exposing the green immature anthers to drying atmosphere raised the frequency of haploids, as well as of hybrids, in common wheat (266). X-raying of the pollen previously to its

application to the emasculated florets seemed to favor the production of wheat haploids (192, 194, 230, 578), increasing the production of haploids in a strain of *T. monococcum* from 0.5% to 13.7% (221). That the pollen, though not fertilizing, may in some way energize the egg to parthenogenetic development was further illustrated by delayed pollination with foreign pollen (221, 222). Emasculated florets of *T. monococcum* were pollinated with pollen from another diploid, *T. aegilopoides*, or with hybrid pollen from the cross of the two wheats. Pollination six days after emasculation gave rise to 20% of haploids, nine days to 37.5%, and five days to none, while emasculation alone produced no seed. Microscopic examination revealed that the egg cell may develop parthenogenetically into a small haploid embryo, and Kihara (221) was of the opinion that further development would cease unless fusion of a sperm nucleus with the polar nuclei arouses endosperm development.

The degree and sometimes type of morphological and physiological response to autopoloid chromosome duplication vary with genus, species and even with the variety (188) and race affected. Auto-"tetraploids" of *Haynaldia villosa* (232), species of *Aegilops* and *Secale cereale* (85, 232) presented a *gigas* habit.

A commonly used criterion for degree of polyploidy is stomatal size. Tetraploids of diploids in *Hordeum* (78, 103, 121, 145), *Secale cereale* (56, 57, 85, 232), *Haynaldia villosa* and species of *Aegilops* (232) showed definite increase over diploids in size of guard cells, an increase in some cases approaching 30%. The large size of epidermal cells causes a correspondingly greater dispersal of the stomata. Breslavetz (57) found the cell and nuclear size in rootlets of autotetraploid *Secale cereale* larger than in the corresponding diploid, triploid and octoploid. Triploid cells ranked second in size. The stomata of the auto-"triploid" *Triticum vulgare* were larger than those of its "diploid" (569). Pollen size also was found to be larger in auto-"tetraploids" (85, 121, 145, 186, 232) and auto-"triploids" (277).

Tabulated comparisons of the diploids and tetraploids of cultivated barleys (78, 121, 145, 185, 186, 188) indicate that all currently desirable qualities may not be in favor of the "tetraploid". In general, the "tetraploids" had somewhat shorter and thicker stems; larger, broader and thicker leaves which at least in some

instances were deeper green (78, 188) ; and possibly in some cases, possessing slightly larger chloroplasts (121). Kostoff (258, 261), in studying the effect of altered euploidy in some members of the Gramineae and Solanaceae, arrived at the conclusion that chloroplast size is independent of chromosome number. Levan (286) found in representatives from 11 plant genera that chlorophyll content per fresh weight in polyploids is usually lower than in diploids and due in part to greater leaf thickness in polyploids. The number of stems in tetraploid barley was apparently variable with race concerned and growth conditions. The rachis was frequently longer but bore fewer flowers which, at least in some races, were larger (188). The number of mature caryopses per rachis was reduced, not only by the smaller number of flowers present but also by the failure of some of the flowers to set fruit. The number of abortive flowers was seemingly determined by plant race (185, 186, 188) and ecological conditions. The total fertility of tetraploids was further diminished by lowered germinability (121, 145, 352). The reduced fertility in barley was in part offset by the larger size and greater weight of grain (78, 121, 186, 188, 352). This grain size relationship held true also in *Avena brevis* (119) and *Secale cereale* (57).

Tetraploidy did not affect the normal self sterility inherent in diploid rye (57). Sengbusch (461), by propagating larger blocks of the tetraploid rye, obtained an increase in yield from 5% or less to 40%.

Flowering of the "tetraploids" was reported as delayed (78, 119) or as simultaneous with diploid, but with prolongation of the open flower period (188). Seed germination was retarded two days or more (78, 121, 145).

Other physiological comparisons recently made in barleys, though not necessarily in agreement (29, 79, 80, 103, 121, 145), point to marked differences between the tetraploid and its corresponding diploid under a given set of conditions. Thus respiration rate was found to be lower (79), while malt diastase activity was twice as great in germinating tetraploid grains as in the corresponding diploid, and catalase activity of the seed powder was two and a half times greater in the tetraploid grains (80). Meagre chemical analyses (79, 103, 145, 352) point to higher contents of proteins (79, 352), ash (79, 103, 145) and sometimes sugars (103) in the tetraploids.

Reactions of autopolyploid plants to external agents and conditions may become significant in interpreting relative survival values of polyploids in nature. Diploid and autotetraploid grains of rye and barley displayed about an equal degree of resistance to high temperature, but the tetraploid survived X-ray treatments with less injury (503). Tetraploid barley survived the X-ray dosages with better germination, vigor and fertility of the resulting plants (350). A number of chlorophyll deficiencies present in the X_2 generation of the diploid were absent from the tetraploid (353).

It is known that the auto-"tetraploid" may display a reaction of its own in hybridization. Autotetraploid *Avena brevis* pollinated by its diploid set no seed; pollinated by *A. sativa* ($2n = 42$) or by *A. barbata* ($2n = 28$) it set seed readily, though diploid *A. brevis* failed to cross with these two species (119). *Secale cereale* autotetraploid ♀ × diploid ♂ produced seed, but diploid ♀ × autotetraploid ♂ was sterile, due to failure of pollen growth (85). *Triticum vulgare* auto-"triploid" ♀ × diploid ♂ set 68.8% of grain, but diploid ♀ × auto-"triploid" ♂ set no grain (569). "Tetraploid" heads of an *Aegilops ovata* chimera, 26.47% fertile when artificially selfed, were 25% fertile when pollinated by "diploid" heads of the same plant (325). However, the "diploid" heads pollinated by the "tetraploid" were only 15.9% fertile.

Karpechenko (188), in enumerating the defects of autotetraploid barleys, mentions the occasional susceptibility to ergot, which was particularly high in one variety.

In meiosis of auto-"tetraploids", bivalents and quadrivalents seemingly vie for supremacy, the preeminence of one or the other being determined evidently by the particular genetic complex involved (78) and, no doubt, also by conditions external to the plant. Autotetraploid *Secale cereale* (85, 232), including the $4n$ part of a chimera (357), viz., *Haynaldia villosa* and species of *Aegilops* (232), produced a mean of one or two quadrivalents, though a maximum of four or five was observed in some forms. Autotetraploid *Hordeum* sometimes displayed the possible maximum of seven quadrivalents with two or three as the mean (121, 401). Auto-"tetraploid" *Aegilops ovata* with 56 somatic chromosomes produced both quadrivalents and bivalents (325). The naturally occurring tetraploid race of *Agropyron cristatum* formed a mean of 3.7% quadrivalents (359); and if quadrivalents are a criterion

for autotetraploidy, both this race of *A. cristatum* and the natural species, *Hordeum bulbosum* with a maximum of seven and a mean of four or five quadrivalents (45, 83), are probably true autotetraploids, each with four identical genomes. Autotetraploid meiosis was often characterized by bridges, higher autosyndetic associations and other indications of structural chromosome changes (78, 379); furthermore, univalents were not always absent. Müntzing (357) observed a lower chiasma frequency in $4n$ than in $2n$ spikes of a *Secale cereale* chimera.

Auto-"triploids" of known origin exhibited also a strong tendency to form trivalents, autotriploids *Triticum monococcum* (230) and *Secale cereale* (257, 277) forming up to four and five or six, respectively. Yamamoto (569) found in the auto-"triploid" *Triticum vulgare* with 63 chromosomes many trivalents of various constructions, but rarely the possible maximum number of 21.

The life expectancy of non-perennial cereal auto-"triploids", characterized as they are by meiotic irregularity in chromosome distribution, is short. Auto-"tetraploids" are usually comparatively stable, but all forms cannot be depended on to breed true. If open pollinated, though only weakly amenable to back-crossing to the corresponding diploid, "tetraploids" may give rise to "triploids" which segregate into diploids and aneuploids. Exclusion of $1n$ pollen did not entirely prevent production of aneuploids in *Secale cereale* (354). In 149 lines of offspring of autotetraploid barley, Chen (78) observed among forms with cytological aberrations, diploids with reduced fertility, hypo- and hypertetraploids, tetraploids with $2n$ and $4n$ pollen in the same anther, and tetraploids with various types of meiotic irregularities. Lines of tetraploids with 14 bivalents had rather high fertility compared with the other groups.

Haploids, according to tables presented by Modilevski (337), now are known in 44 genera representing many families. Haploidy in angiosperms is discussed also by Ivanov (166).

The haploid in cereals is usually a less robust replica of its diploid parent, and has in some cases been recognized by smaller and less dispersed stomata (568). According to Yefeikin and Vasiliev (557, 578), haploids of the durum or tetraploid group of wheat, as *T. persicum* and *T. dicoccum*, bore striking resemblances to wheats of the einkorn or diploid group in respect to head charac-

ters and conspicuous nodal pubescence. It may be relevant in relation to these results that Camara (67), in reviewing the interrelationships of wheat, noted that some wild diploid species, especially *T. Thaoudar*, show very close resemblance to *T. dicoccoides* and others of the tetraploid series. The latter author suggested that tetraploid species of wheat may have arisen from diploid by chromosome duplication followed by chromosome changes. Having observed the results of X-rays, he thought it possible that through simple processes of evolution, as fragmentation, translocation and other structural changes, there could be constructed from the chromosomes of the diploid the complete series of chromosomes of the tetraploid.

The usual great preponderance of univalents in the first meiotic division in haploids has been further confirmed in the diploid species *Triticum monococcum* (230), *Hordeum distichum* (531) and *Secale cereale* (285, 375); in the tetraploid species *A. ovata* (325) and *T. durum* (213); and in the hexaploid species *T. vulgare* (257, 274, 288, 429, 568, 572). The approximate average, based on calculable reports, of pollen mother cells with univalents exclusively is 80% in diploid and tetraploid species, and drops to 60% in the hexaploid *T. vulgare*, indicating, perhaps, inclusion in the hexaploid of more chromosomes with partial homology. However, there are various other factors that apparently govern pairing in the haploid. Some of these are external; others, including genetic, are internal. Levan (285), in a comparative study of three haploid rye individuals, observed that pairing varied from plant to plant, and in one instance from locule to locule. Two of the haploid individuals presented ten times the number of chiasmata of the third.

Haploids, in cereals, like triploids are cytologically highly unstable and perish after flowering, or revert to "diploids" through formation of restitution nuclei in the germ cells. The reverted "diploids", according to Kostoff (266), may not, though selfed, be heterozygous, as crossing-over between autosyndetically conjugated chromosomes may lead to structural chromosome changes. Segregation of morphological and physiological characters occurred in reverted "diploids" of *T. vulgare*. Sears (450, 451, 455, 457) found that the progeny of haploid *T. vulgare*, when pollinated by the "diploid", produced an excellent source of cytological aberrations, including nullisomics and polysomics. Some of the aber-

rations were accompanied by definite phenotypic effects. Use of chromosome aberrants in "diploids" derived from haploids has proved to be a successful method of analyzing *T. vulgare*, and Sears suggests that other supposedly polyploid plants may be amenable to this same sort of analysis.

Undoubled Interspecific Hybrids

Data on cytology of hybrids has been augmented markedly and especially in the field of amphidiploidy. A brief summary, covering reports to 1937, on chromosome pairing in specific and generic cereal hybrids has been compiled into a serviceable 21-page table (214). Other summaries covering also some more recent work are available (86, 149, 265).

Cytology of interspecific hybrids in *Triticum* covers crosses within a chromosome group, as diploids (496), tetraploids (31, 39, 74, 84, 86, 87, 234, 238, 243, 307, 516) and hexaploids (88, 105); and crosses between chromosome groups, as diploid \times tetraploid (31, 238, 239) and tetraploid \times hexaploid (49, 86-88, 106, 147, 160, 168, 238, 302, 390). Some of these hybrids involve, besides the hexaploid *T. Macha* (88), two newly discovered Chinese tetraploids, "blue" wheat and dwarf hill-wheat from Szechwan (87). Of the hexaploid crosses, *T. Macha* \times *T. vulgare* was weak and failed to form pollen mother cells (88), and *T. Macha* \times *T. spelta* was 63.5% sterile and at meiosis produced 13-21 bivalents. Univalents, rings of four or six or chains of three or five chromosomes, and bridges were present. Apparently *T. Macha* differs somewhat both cytologically and genetically from other known hexaploid wheats. *T. Macha* \times tetraploid wheats differed little from other pentaploid crosses except the cross involving *T. dicoccum* as the second parent which was almost sterile due to crumbling of chromosomes at the end of the second division.

The hoped-for goal of combining the most desirable agricultural qualities of hexaploid wheats with the high disease resistance of some tetraploid wheats has led to the continuance of extensive work on pentaploid wheat offspring (144, 147, 217, 226, 229, 298, 299, 301, 303, 310-316, 323, 324, 327, 384, 398, 442, 443, 462, 521, 575, 576), including back-crosses (37, 317-321, 324, 462, 575).

Cytological data on interspecific hybrids in *Aegilops* have with some exceptions (46, 292, 454, 505) been augmented by Kihara

and his collaborators (167, 214–216, 219, 225, 227), and have been summarized (214) and discussed by Kihara in relation to a new classification scheme (218, 220, 223) based in part on cytogenetical results. The genus is divided into six sections, and each section, unlike in *Triticum*, may contain more than one chromosome group. The species in a section are thought to have at least one genom in common.

Secale cereale × wild *Secale* species had seven bivalents and showed high fertility, except *S. secale* × *S. montanum* which had five to seven bivalents (245) and some other chromosome irregularities, and suffered consequent reduction in pollen fertility (102). Kostoff (245) pointed out the value of *S. ancestrale* as a robust and productive species worthy of trial in a hybrid with *S. cereale*.

Interspecific hybrids in *Hordeum* have recently been reported (427).

Little is known as to the cytogenetical relationships within the comparative large genus *Agropyron*. Cytology has been described for apparent hybrids, of spontaneous origin from five localities in Sweden, between tetraploid *A. junceum* and hexaploid *A. repens* (381, 383). Seven plants were pentaploid, as expected, and at meiosis had nine to 13 bivalents in addition to univalents. Plants from one locality were heptaploid, having arisen presumably through back-crossing of the pentaploid hybrid to *A. junceum*, or through fertilization of an unreduced *A. junceum* gamete by *A. repens*. Both hybrids were heterozygous for inversions, and both were highly sterile. Also other probable *Agropyron* hybrids of natural origin have been discovered (480, 481).

Some interspecific *Avena* hybrids within the diploid and tetraploid chromosome groups produced, besides bivalents, a ring of four chromosomes, explained on the basis of segmental interchange (108, 110). Diploid × tetraploid formed five to seven pairs (109, 368, 464) and showed decreased fertility. Chromosome morphology (464) and general cytogenetic characteristics point, however, to a close relationship between species of the diploid and tetraploid chromosome groups (111). Tetraploid *A. barbata* (AAB'B') × autotetraploid *A. strigosa* (AAAA) formed seven bivalents contributed by homologous genomes AA, and, in addition, five or six bivalents derived through pairing between partially homologous genomes A and B' (370). The formation, on the average, of more

than seven bivalents in diploid *A. longiglumis* \times hexaploid *A. sativa* (109) also substantiates the incidence of autosynopsis. Comparatively low pairing and high sterility characterized pentaploid oat hybrids, as *A. fatua* and *A. barbata* (373). An octoploid plant with 28 bivalents arose among other F_4 progeny of the back-crossed pentaploid, but did not breed true.

Undoubled Intergeneric Hybrids

The majority of intergeneric crosses in small-grain cereals involve the genus *Triticum* as one parent.

Compared with *Aegilops cylindrica*, other *Aegilops* species showed apparently less chromosome homology with species of *Triticum*, though a variable number of bivalents, usually of the open formation, were present (195, 214, 390, 453, 454, 507). Tests made by Miège (333–335) suggested that the introduction of *Aegilops* into wheat may improve its baking quality. Species of *Aegilops* as well as *Haynaldia villosa* contained more mineral matter, nitrogen and gluten, and less starch than wheat.

The genomes of diploid *Haynaldia villosa* (214, 228, 238, 239, 453, 454) and *Secale cereale* (214, 290, 363) met little or no homology in crosses involving species of *Triticum*. The tetraploid *Haynaldia hordeacea* Hack., an extremely hardy and drought-resistant perennial, in serving as ♂ parent in a cross with Vjatka rye, gave rise to a fertile hybrid (598).

Among desirable characteristics (98, 147, 329, 434, 438) obtained in different wheat-rye hybrids and their segregates have been various types of disease resistance, cold and drought tolerance, early maturity and good grain quality.

Some species of *Agropyron* cross with *Triticum*, and apparently more successfully when *Triticum* is the ♀ parent. Cytology of *Triticum* \times *Agropyron* is known in hybrids including tetraploid and hexaploid chromosome groups of *Triticum*; and four species of *Agropyron*, namely, the tetraploid and hexaploid races of *A. intermedium* (syn. *glaucum*) (35, 208, 209, 400, 405, 424, 488, 535, 541, 556), the tetraploid race of *A. junceum* (382), the hexaploid *A. trichophorum* (305) and the decaploid *A. elongatum* (208, 209, 400, 404, 405, 423, 424, 540, 548–551, 553, 555). Variations in meiotic chromosome configuration occurred in all combinations, indicating incomplete homology between *Triticum* and *Agropyron*.

genoms, and also a difference in the response of ecotypes and races entering into a particular cross. The maximum number of possible bivalents was approached more often in the F_1 with the highest chromosome number. Autosyndesis between two *A. elongatum* genoms was apparently responsible for the large number of bivalents when this decaploid species entered the cross (209, 400, 548, 549). Assumption of the quadruple state of one genom of *A. elongatum* seems to be substantiated by the finding of an average of three quadrivalents and frequently a ring of eight chromosomes in the spore mother cells of a race of this species (400). Other high chromosome aggregates, in addition to about 22 bivalents and two univalents, were also found.

Irregularities in meiosis of the hexaploid *A. intermedium* (syn. *glaucum*) suggest previous interchange of segments between non-homologous chromosomes. The tetraploid race of *A. intermedium* apparently lacks at least one type of genom found in the hexaploid race (400, 548). The phenotypic effects of the exclusion or inclusion of a genom has evidently not been of such magnitude as to give the two races separate specific rank.

Two F_1 plants of *T. durum* ($2n = 28$) \times *A. trichophorum* ($2n = 42$), though quite similar as to morphology and high rust resistance, were markedly divergent as to meiotic chromosome behavior (305). One plant had a large number of univalents and an average of 1.6 bivalents per sporocyte; the other plant had an average of 6.06 bivalents and frequently a chain of three chromosomes, and inversion bridges were present in 4% of the cells. As little was known as to the chromosomal constitution of the two parents, it was impossible to decide whether the differences found in the two plants should be ascribed to strain differences in the parents, or to the functioning of antipairing genes in one of the plants. *T. Macha* ($2n = 42$) \times *T. trichophorum* ($2n = 42$) produced an average of 7.7 bivalents per sporocyte and frequently chains of three or four chromosomes. Inversion bridges were present in 25% of the cells. The fertility of all the hybrids involving *A. trichophorum* was extremely low. Crosses are reported to have been obtained also between *Triticum* species and *A. obtusiuscum* (*sic*) (270).

Fertility in *Triticum-Agropyron* crosses has been variously described as low to comparatively high, and has often bettered with succeeding generations. The agronomic values apparently depend

on races of *Triticum* and *Agropyron* entering the cross. Some of the more meritorious characteristics observed, singly or in various combinations (89, 143, 430a, 439, 459, 465, 479, 492, 536, 538, 539, 541, 543, 561-563), are high protein content of grains, superior baking qualities, large grains, high grain yield, standing capacity, early maturity, drought and saline tolerance, and rust and smut resistance. Some segregates are annual, others perennial. Some may produce a good hay crop in addition to the grain harvest. The *Triticum-Agropyron* cross, like other intergeneric crosses, is still in the early experimental stage.

Hybrids between *Triticum vulgare* ($2n = 21$) and *Elymus arenarius* ($2n = 56$) were obtained when each parent plant had developed from an embryo grafted onto the endosperm of the foreign genus (411).

Meiosis in the diploid hybrid *Haynaldia villosa* \times *Aegilops* indicated only little chromosome homology (46, 214) between the two genomes.

The hexaploid race of *Agropyron intermedium* in crosses with diploid, tetraploid and hexaploid species of *Aegilops* produced numbers of bivalents approaching the possible maximum (116), and is cytologically as close, it seems, to these *Aegilops* species as it is to *Triticum*.

Secale cereale, in crosses with tetraploid species of *Aegilops* (214) and the hexaploid race of *Agropyron* (540), presented a higher bivalent formation than in crosses with species of *Triticum* with which it apparently has no chromosomes in common. Crosses have been obtained also between *Secale* and the following species of *Agropyron*: *repens*, *sibiricum*, *trichophorum* (491) and *cristatum* (93, 272).

Hordeum distichon var. *nutans* Schübl. ($2n = 14$) $\text{♀} \times$ *Elymus giganteus* ($2n = 28$) ♂ produced a hybrid plant with 21 chromosomes (39a).

Back-crossing in intergeneric hybrids, as *Triticum* \times *Secale* (120, 196, 197, 200, 202, 281, 533) and *Triticum* \times *Agropyron* (208, 211, 405, 533), resulted in various chromosome combinations and sometimes in sesquidiploids (208, 209, 211) and amphidiploids (120).

Use of later generations of hybrids to pollinate F_1 hybrids (380, 541) has in some instances been preferable to back-crossing to improve fertility as well as to bring about favorable segregates.

Triticum \times *Secale* progeny (196, 197, 199, 200, 202, 203, 281) has served in studies of genom stability.

Interspecific Amphidiploids

Amphidiploidy, arising, generally speaking, through recovery of genom "diploidy" from aberrant allopolyploid genom haploidy, has no doubt played an important rôle in the building of natural species; and increased ingenuity in the use of polyploidogenic agencies will greatly multiply the number of amphidiploids in selected genera.

Triticum crosses elevated from triploids to hexaploids through amphidiploidy are: *T. durum* ($2n = 28$) \times *T. monococcum* ($2n = 14$) (581, 583, 585, 591, 595), named *T. Edwardi* Zheb. (594); *T. Timopheevi* ($2n = 28$) \times *T. monococcum* ($2n = 14$), named *T. Timococcum* (236, 254); and *T. persicum* ($2n = 28$) \times *T. monococcum* ($2n = 14$) (191). Amphidiploids of the octoploid series are: *T. polonicum* \times *T. durum* (584); *T. Timopheevi* ($2n = 28$) \times 28-chromosome wheats of different species and varieties (582, 583, 586, 589–595), all named *T. soveticum* Zheb., the 28-chromosome parent entering the cross with *Timopheevi* supplying the subspecies name, e.g., *T. soveticum* ssp. *durum* (589, 594). Amphidiploid *T. Timopheevi* \times *T. persicum*, included in above group, has been designated as *T. fungicidum* by another author (597, 598) to signify its high resistance to fungal diseases. The amphidiploids in this octoploid series involving *T. Timopheevi* as one parent are generally characterized by high disease resistance and very large grain (582, 596, 597). An exception in respect to disease resistance is *T. Timopheevi* \times *T. orientale* which derives a susceptibility to mildew from *T. orientale* (592), a species of low resistance to mildew and rust, low adaptability and limited distribution. The different hybrids of the octoploid series intercross readily (594). In the decaploid series are amphidiploids *T. Timopheevi* ($2n = 28$) \times *T. vulgare* ($2n = 42$) (587, 591, 595), named *T. Borisovi* Zheb. (594), and *T. durum* ($2n = 28$) \times *T. vulgare* ($2n = 42$). A dodecaploid amphidiploid *T. vulgare* ($2n = 42$) \times *T. compactum* ($2n = 42$) has been reported (99). *Triticum* amphidiploids, like amphidiploids in general, present in varying degrees a less regular meiosis and lower fertility when compared with well established species.

In the genus *Aegilops* hexaploid (220) and numerous tetraploid (216, 232, 328, 449, 453, 454) amphidiploids have been developed.

Amphidiploid *Ae. caudata* ($2n = 14$) \times *Ae. squarrosa* ($2n = 14$) has been described as a plant similar to *Ae. cylindrica* ($2n = 28$) in respect to morphology and chromosome constitution (328). *Ae. cylindrica* is thought to contain the C genom in common with hexaploid wheats, and possibly also in common with *Ae. squarrosa*, and to contain a second genom in common with *Ae. caudata*.

Intergeneric Amphidiploids

The first cereal amphidiploids cytologically studied were all intergeneric, as *Secalotriticum* (or "Triticale"), *Aegilotriticum* and "Haynaldtricum".

A hexaploid amphidiploid, *Triticum durum* ($2n = 28$) \times *Secale montanum* ($2n = 14$) (97, 98), has been said to be a vigorous, drought-tolerant, disease-resistant and high grain-yielding perennial. Octoploids of the *Secalotriticum* type, amphidiploid *T. vulgare* ($2n = 42$) \times *S. cereale* ($2n = 14$) (47, 99, 147, 159, 344, 364, 552) have been produced, one by double back-crossing [*T. vulgare* \times *S. cereale*) $F_1 \times T. vulgare$] $F_1 \times S. cereale$, and apparently the result of the fertilization of an unreduced egg at each of the last two steps (120).

Müntzing (349), in a comparative study of six strains of *Triticum-Secale* amphidiploids from diverse sources, found that the strains differed from one another as to vigor, fertility, meiotic stability and general physiological and chemical aspects, and that they intercrossed with greater difficulty than different varieties of wheat. The direction of the cross was sometimes a deciding factor. Ease of self-fertilization is apparently inherited from the *Triticum* parent. Chemical analyses (273, 349, 438) disclosed that *Secalotriticum* differed from the corresponding undoubled hybrid as to grain qualities. The future agronomic worth of the wheat-rye amphidiploid seems subject to diverse opinions. Müntzing (352) regards present types an improvement over the old.

Amphidiploids of *Triticum* \times *Aegilops* have been developed between several chromosome series of the two genera. Sears (453, 454) has made a more extensive study of the tetraploid group. From cross to cross the average number of multivalents and univalents varied from 0.24 and 0.12, respectively, per sporocyte to 4.72 and 1.60, and with this increase in mitotic irregularity the corresponding percentage of non-abortive pollen dropped from 93.5 to

76, and the grain set dropped from 94 to 25. *Aegilotriticum* octoploids of various species combinations have been developed (376, 394, 458, 504, 506, 507). Amphidiploid *Ae. cylindrica* ($2n = 28$) \times *T. turgidum* ($2n = 28$) in a cross with *vulgare* had 21 bivalents + seven univalents at meiosis, as should be expected if *Ae. cylindrica* and *T. vulgare* both possess the C genom. When *Ae. cylindrica* was replaced by *Ae. ventricosa*, homology seemed confined to fewer chromosomes, or to parts of chromosomes only (458). The frequent occurrence of trivalents and quadrivalents may possibly be explained by the behavior of *ventricosa* in a cross with another tetraploid wheat. The 42-chromosome sesquidiploid *Ae. ventricosa* ($n = 14$) \times *T. dicoccum* ($14 + 14$) resulting from the back-cross to *T. dicoccum*, produced at meiosis 14 dicoccum bivalents and seven autosyndetic *ventricosa* bivalents (507). When the sesquidiploid was crossed with *T. vulgare*, usually 21 bivalents were formed and the fertility was 65%. With *T. spelta* as the hexaploid wheat parent the fertility rose to 86%.

The assumption that the C (or D = dinkel) genom of hexaploid wheats is of *Aegilops* origin has led to attempts to synthesize these wheats. The problem at present apparently is to locate a diploid species with the C genom either practically unaltered or altered along the pattern of the C genom of *Ae. cylindrica* and hexaploid wheats. Such an *Aegilops* species in an amphidiploid cross with most 28-chromosome wheats should be expected to give rise to a hexaploid plant generally similar morphologically and physiologically to the existing hexaploid wheats of natural origin. One such plant approaching the theoretical form, developed by Britten and Thompson (64, 524), was amphidiploid *T. durum* ($2n = 28$) \times *Ae. speltoides* ($2n = 14$). It had the same chromosome number as *T. vulgare* and crossed readily with this species, without much consequent meiotic irregularity or lowered fertility. The amphidiploid differed from *T. vulgare* by a few minor morphological features, less meiotic regularity and lowered fertility. Doubt has been raised as to the possession of the C genom by *Ae. speltoides*, and A' has been proposed as a substitute genom (436) on account of rather high bivalent formation in the undoubled hybrid and the presence of four nucleoli in *Ae. speltoides*. Four nucleoli have also been found in some diploid wheats which have been credited with the diploid genom formula AA. The above hybrid should therefore possess a

maximum of eight nucleoli, whereas the *vulgare* wheats possess a maximum of six.

Another synthetic hexaploid, developed by McFadden and Sears (328), was amphidiploid *T. dicoccoides* ($2n = 28$) \times *Ae. squarrosa* ($2n = 14$). This plant has been described as stable, highly fertile and morphologically almost identical with *T. spelta*, and in a cross with the spelt formed 21 bivalents in about half of the sporocytes, with multivalents rarely occurring. The performance of *Ae. squarrosa* in producing the synthesized copy of *T. spelta*, as well as that of *Ae. cylindrica* [see tetraploid *Aegilops* amphidiploids (328)], suggested to the above authors that *squarrosa* may carry the $2n$ genom formula CC.

McFadden (327a) has reported still other hexaploid amphidiploids in the *Triticum* ($2n = 28$) \times *Aegilops* ($2n = 14$) group.

Naturally occurring *Aegilotriticum* forms have been found in France (75), and apparently undoubled *Triticum-Aegilops* hybrids in wheat fields of Spain (158) and in other countries (101). Some forms of *Triticum-Aegilops* amphidiploids have been described as free from lodging and shedding (9).

Amphidiploid *Haynaldia villosa* ($2n = 14$) \times *Triticum dicoccum* ($2n = 28$), named *Haynaticum* (598), is a self-pollinated annual with vitreous grains exceeding in length those of either parent.

The most sterile amphidiploid reported within the scope of this review is *Aegilops umbellulata* ($2n = 14$) \times *Haynaldia villosa* ($2n = 14$) with no grain set, in spite of low pairing in the undoubled hybrid and few multivalents in the amphidiploid. More than half of the chromosomes in the amphidiploid meiosis remained unpaired (454).

Decaploid amphidiploids *Triticum* spp. ($2n = 28$) \times *Agropyron intermedium* (syn. *glaucum*) ($2n = 42$ race) have been induced artificially, but the amphidiploid number in some of these crosses apparently readily arises spontaneously through selfing of unreduced gametes in the undoubled hybrid (157, 210). Meiotic regularity varies, possibly with races entering the cross, and growth locality. Bivalents ranged in number from 27 to 35 with a corresponding number of univalents and occasional multivalents (36, 157, 406). The plants have been described (157, 210, 211) as sturdy, luxuriant, rust-resistant, non-stoloniferous, highly fertile perennials, offering a cereal-grass of immense value, at least for fodder. The flowers

are open-pollinated, but close-pollination does not reduce fertility. This series of amphidiploids has been grouped under the name *Agrotriticum*, the wheat species of the cross adding the species name, e.g., *Agrotriticum durum* (211). Dodecaploid-amphidiploid *T. vulgare* ($2n = 42$) \times *A. intermedium* ($2n = 42$) has also been obtained (402, 403, 407, 430).

Amphidiploids have been used to advantage in pollinating sterile undoubled hybrids, depending for success on the chance fertilization of an unreduced ♀ gamete of the primary F_1 hybrid by a reduced ♂ gamete of the amphidiploid (198, 206, 349, 386). The number of strains of amphidiploids may also be increased in this manner.

Back-crossing in amphidiploids (193, 195, 284, 349, 378) depended in part on parental races and direction of the cross for success and fertility.

Phenotypic expression of amphidiploidy in cereal crosses has been briefly referred to under the respective crosses. An almost infallible reaction to chromosome doubling in the primary cross is some degree of increased fertility (454) which in some series, it seems, is more apparent in the lower chromosome groups. The 42- and 56-chromosome wheat amphidiploids had generally a higher fertility than the 70-chromosome (594). However, other causes besides high polyploidy apparently lower fertility. Sears (454), in comparing the characteristics of 18 amphidiploids of diploid interspecific and intergeneric hybrids in *Triticinae*, observed that fertility varied from nearly perfect to almost zero. Also, there was no consistent relationship between the fertility of the amphidiploid and the lack of pairing in the undoubled hybrid.

Size and vigor of plant, thickness and greenness of leaf, maturity time, disease immunity, size and composition of grain, baking quality of meal, and general responses to external surroundings were apparently conditioned by the two components of the cross.

The grain size of fertile amphidiploids frequently was larger than that of the parents (247, 598). Sears (453) found that 12 of 17 tetraploid amphidiploids, interspecific and intergeneric, had grains exceeding in size those of either parent. The 1,000-grain weight of amphidiploid *Triticum orientale* ($2n = 28$) \times *T. Timopheevi* ($2n = 28$) was 80 to 95 grams, with selected grains attaining 100 to 110 grams (591, 594), and exceeding the grain weight of either parent. Sears (453) found that intergeneric amphidiploids showed

generally less increase over parental averages than interspecific. The 1,000-grain weight of amphidiploid *T. vulgare* ($2n = 42$) \times *Agropyron intermedium* ($2n = 42$) was 10 to 20 grams, and intermediate between the 32 to 37 grams of *T. vulgare* and 5 to 6 grams of *A. intermedium* (407).

Flowering date is usually postponed with increasing degree of polyploidy. Kostoff (247) observed that diploids bloom later than haploids, tetraploids later than diploids, and amphidiploids later than the primary undoubled hybrid. Amphidiploids of winter varieties of *Triticum vulgare* \times *T. Timopheevi* were late ripening spring wheats (594). Wheat amphidiploids generally had a longer vegetative period than their parents, and some combinations acquired greater capacity for winter survival (594). That polyploid plants are generally possessed of a greater degree of hardness has not been confirmed by Bowden (54). Chromosome doubling may secondarily affect the hardness of a plant, but it is thought that genic mutation and hybridization bring about most of the variation in degree of resistance to cold. Löve and Löve (295), however, through a statistical study came to the conclusion that the percentage of polyploids in the flora increased with latitude. The perennial and biennial habits of plants in a genus, according to Müntzing (343) in a study of 582 species, including 48 genera, are more often associated with a higher chromosome number. The average gametic chromosome number of perennial plants was 16.95, of biennial and sub-perennial 15.5, and of annual 10.65.

Randolph (428) has suggested that increased chromosome duplication in already highly polyploid plants may be detrimental rather than beneficial. Most cultivated forms of wheat and oats are natural hexaploids, and further doubling leads to dwarfness and various deformities as well as high sterility. Kostoff (255, 256) is of the opinion that high polyploidy, and especially autopolyploidy, in plants with long chromosomes, as in the small-grain cereals, tends to lead to sterility, due in part to higher chiasma frequency and hence more multivalents and irregular chromosome distribution at meiosis. Highly polyploid plants with short chromosomes, therefore, should have a better chance of survival. Numerous evidences were drawn from natural polyploids with short and with long chromosomes. It may be pertinent in this connection that Marshak and Bradley (308) found the total chromosome length in the nuclei

of natural wheat species decreased per genom with the increase in polyploidy. The mean aggregate length of the metaphase chromosomes of a root-tip nucleus was $118\ \mu$ in *T. monococcum* ($2n = 14$), $203\ \mu$ in *T. dicoccum* ($2n = 28$), and $248\ \mu$ in *T. vulgare* ($2n = 42$).

Stomatal size and distribution, generally fair indicators for autopolyploidy in cereals, seemed not too reliable as a test for amphidiploidy. Amphidiploid sectors of *T. monococcum* \times *Ae. uniaristata* indicated no deviation from the undoubled hybrid as to stomatal size and distribution. Amphidiploid *Aegilopoides* \times *Ae. umbellulata* showed generally fewer stomata per unit area, while amphidiploid *Ae. caudata* \times *Ae. umbellulata* and *Ae. speltoides* \times *Ae. umbellulata* had definitely larger and sparser stomata (449, 453). Stomatal size of decaploid *Triticum-Agropyron* amphidiploids exceeded that of the undoubled hybrids (406). The amphidiploid *Secale montanum* \times *T. durum* had larger stomata than either of its parents (599). The mean stomatal length in *Triticum* was found to have increased with the natural increase in polyploidy from $41.7\ \mu$ in diploids, to $46.1\ \mu$ in tetraploids, and $53.3\ \mu$ in hexaploids (51). The stomatal number per unit area correlated inversely at 82.1 per sq. mm. for diploids, 63.9 for tetraploids and 46.6 for hexaploids.

Pollen grain volume, another indicator of cell size, presented in 56-chromosome *Aegilotriticum* and its parents, *Triticum dicoccoides* and *Aegilops ovata*, a ratio of 2.47, 1.30 and 1.00, respectively (193). The pollen grain size apparently correlates with natural increase in polyploidy in the genus *Triticum*, for although variations occurred within a chromosome group the length and width in diploids averaged 47.7×41.2 microns, in tetraploids 54.4×47.6 , and in hexaploids 61.7×54.3 (509).

The chromosome stability of amphidiploid offspring, in general, is variable with race combinations of the undoubled cross. Sears (454), in a tabulation of 21 different interspecific and intergeneric amphidiploids in the tetraploid group, found that out of 144 offspring 29 were monosomics, five were trisomics and the balance were of regular chromosome constitution. The preponderance of monosomics was attributed to loss of chromosomes during meiosis.

Sesquidiploids or Haplo-Diploids

In sesquidiploids the chromosome complement of one component of the cross has attained diploidy and the other has remained

haploid. Sesquidiploids have been assumed to have arisen in several ways but usually through the fertilization of an unreduced gamete by a reduced gamete. The unreduced ♀ gamete may have been that of a natural species, as in case of the 49-chromosome sesquidiploid *T. dicoccum* $(14+14)♀ \times T. vulgare$ ($n=21$) ♂ (168), or the unreduced ♀ gamete of a hybrid which on backcrossing to one of the parents has given rise to the sesquidiploid (50, 208, 209, 211, 281, 507). The parentage of the doubled complement can be inferred when the chromosome numbers of the two parents differ, and while it has generally been the ♀ gamete that has remained unreduced, cases have been reported in which the ♂ gamete may have remained unreduced, as indicated in the 35-chromosome sesquidiploid *T. vulgare* ($n=21$) ♀ $\times T. monococcum$ $(7+7)$ ♂ (234), or two sperms may have functioned, as suggested for the origin of the 49-chromosome sesquidiploid twin seedling *T. vulgare* ($n=21$) $\times T. armeniacum$ $(14+14)$ (190).

Triple Hybrids and Bridge Crosses

Some species do not cross directly with one another, but their chromosomes can be brought together through an intermediary bridge cross. Thus *Secale cereale* \times *Haynaldia villosa* ended in failure, but [*Triticum dicoccum* (genoms AB) \times *Haynaldia villosa* (genom V)] $F_1 \times$ *Secale cereale* (genom S) ♂ resulted in a robust trigeneric hybrid possessing characters of the three component genera (238, 267, 268). The 28 chromosomes, representing the complete genom sets of the three genera, remained as univalents in about 90% of the sporocytes, indicating little or no homology among the genoms ABVS. The success in bringing together the complete genoms in a triple hybrid of this type depends on the occasional formation on an unreduced ♀ gamete, probably through a restitution nucleus in the F_1 of the primary or bridge cross. Selfing of spontaneously unreduced gametes of the trihybrid, or subsection of plant to a polyploidogenic agency should bring into being a fertile trigeneric octoploid amphidiploid with the genom formula AABBVVSS.

A sterile perennial F_4 wheat-*Agropyron* plant with a somatic chromosome number of 48 pollinated with pollen of *Elymus giganteus* ($2n=28$) gave rise to a trigeneric hybrid with 52 chromosomes. It was inferred that an unreduced ♂ gamete may have participated in the fertilization (508a).

It is desirable to transfer the high disease resistance of the Russian wheat *T. Timopheevi* to hexaploid wheats, but the two wheats do not cross successfully. However, [*T. spelta* (ABC) \times *T. polonicum* (AB)] $F_1 \times T. Timopheevi$ (AG, or AB) σ^7 was highly fertile with 28–34 and possibly 35 chromosomes (212). The highest number, 35, should represent the A and B genomes from paired, and C genome from unpaired chromosomes of the primary F_1 , in addition to AG (or AB) genomes of *T. Timopheevi*. Through the pentaploid bridge cross the genomes of *T. vulgare* and *T. Timopheevi* were brought together. Similarly sterility in *T. monococcum* ($n=7$) \times *T. vulgare* ($n=21$) was avoided by the previous introduction of a 28-chromosome wheat into a bridge cross with *T. monococcum* (234, 237).

The comparatively frequent formation of unreduced gametes in the F_1 of some of the *Triticum-Agropyron* crosses made these crosses on pollination with a third species amenable to the inclusion in a triple hybrid of the complete haploid genom sets of three species (208, 209, 211). As the unreduced gamete of the primary undoubled hybrid and the reduced gamete of the amphidiploid are identical, the triple hybrid type resulted also on crossing an amphidiploid hybrid with a third species, as briefly discussed under *Triticum-Aegilops* amphidiploids (328, 458, 507, 524). A number of other triple hybrids have been described by Vakar (554).

CHROMOSOME MORPHOLOGY AND GENOM RELATIONSHIPS

The present methods of attack on cereal chromosome morphology are laborious and possibly not always proving directly as fruitful as hoped for in unraveling problems of phylogeny. The difference in chromosome size is not outstanding, and divergence in arm length occurs to the same degree in too many chromosomes. Satellited constrictions with or without nucleoli, and secondary constrictions in general, should perhaps be some of the most tangible means for the identification of cereal chromosomes; but many of these constrictions often either elude detection or may possibly be simulated by artifacts. The reports are at least conditioned by cytological procedures and possibly by race and ecological conditions. Levan (285) found that in *Secale cereale* one pair of satellites was observed readily, a second pair with greater difficulty, and that by exposing growing root tips to 0° C. for one to three days, additional

satellite-like bodies appeared at the ends of the chromosomes. The latter bodies brought out by cold treatment were possibly heterochromatic and their visibility due to nucleic acid starvation induced by low temperature treatment.

Triticum monococcum has been credited variously with none to four or more pairs of satellited chromosomes (67, 104, 388, 389, 495), and observations as to secondary constrictions in general have been far short of unanimous. The average of obtainable reports indicates that the number of total secondary constrictions may be approximately the same in diploid, tetraploid (49, 67, 74, 104, 160, 182, 184, 205, 223, 285, 388, 389, 464, 466, 495) and hexaploid (49, 223, 388, 464) chromosome groups, including species of *Triticum*, *Hordeum*, *Secale*, *Aegilops* and *Avena*. Tandem satellites have been observed in a pair of chromosomes in *T. dicoccum* and *T. vulgare* (49). The maximum number of nucleoli was observed to be one per genom of seven chromosomes in diploid *Secale cereale* (388); tetraploids, *T. dicoccum* (49), *T. durum* (182, 184, 388), *Aegilops cylindrica* and *Ae. ovata* (388); and hexaploids, *T. vulgare* (49), *T. spelta* (388), *Ae. crassa* (388) and *Agropyron repens* (463). The diploids, *T. monococcum*, *T. aegilopoides* and *Ae. speltoides*, were exceptions in that they had two nucleoli per genom. Pathak (388) interpreted the presence of a maximum of two nucleoli per genom in some diploids as additional support of the theory that five is the basic number, and that seven is a secondary derivation in the Gramineae. Bhatia (49) found two large and two small nucleoli in *T. dicoccum*, four large and two small in *T. vulgare*, and suggested that the difference in size as well as staining reaction may be explained by the difference in origin of their respective genoms.

Kakhidze (182) investigated the possibility of chromomere arrangement in the pachytene of microsporocytes of *T. durum* as a method of comparing chromosome homology. Two pairs of SAT-chromosomes, distinguished from one another by the nucleolar contact body, were selected for comparison. Small sections on either side of the contact body showed differences in the two pairs as to sequence arrangement of large and small chromomeres, but whether these differences point to non-homology or to regrouping due to inversions can be determined only after the entire chromosomes have been studied.

Bodies designated as compound chromomeres have been differentiated in early and late metaphase of mitotic chromosomes of rye root tips subjected to 0° C. for 24 hours, fixed in strong platinum-formalin or other suitable reagents and critically differentiated in the staining procedures (467, 468). The cold treatment also brought out secondary constrictions in addition to compound chromomeres (466). The compound chromomere was regarded as an aggregate of ultimate chromomeres. Shmargon (467) calculated that in the nucleolus-bearing SAT-chromosome of rye, approximately 50 ultimate chromomeres of the meiotic pachytene in the sporocyte were condensed into 11 compound chromomeres or packets of the early or late mitotic metaphase of the root tip. In split portions of the thread the size and distribution of compound chromomeres were identical (468). The shortest chromosome of the rye genom contained nine compound chromomeres, and the longest 13. The number of chromomeres between chromosome constrictions was constant. Comparisons of compound-chromomere arrangement in an appendaged chromosome of two varieties of *T. durum* revealed that a structural deficiency had occurred as to one of the chromosome arms of one variety (184).

Kostoff (246, 248, 249), through critical stain differentiation, observed deeply staining bodies which were grouped more closely at the ends of mitotic chromosomes in wheat. He interpreted these bodies as heterochromatin, and as possibly inert with the genes located between them.

Genom formulae generally evolve from studies of meiotic pairing in hybrids and comparisons of chromosome morphology in species. They may at best be considered as useful though perhaps only temporary markers of progress in classification and interpretation of added data. The use of different races under diverse conditions naturally precludes unanimous results and interpretations, thus rendering the problems more elusive, but perhaps also more challenging.

Idiograms indicate that 14 chromosomes, presumably genomes A and B, of *T. vulgare* resemble closely the chromosomes of *T. dicoccum* (49) and *T. polonicum* (287). Chromosome morphology as well as apparent autosynopsis in hybrids seem to indicate that three chromosomes in the A genom may closely resemble three of the B genom (287), but the chromosomes of the C (or D = dinkel)

genom are all unlike those of the A and B. The B genom of two tetraploid wheats *T. Timopheevi* and *T. armeniacum* has a limited homology with the B genom of other tetraploid wheats and has been designated as genom B (238-241, 243) or genom G (220, 425, 516). Kihara (220) has suggested that hexaploid wheats derived the AB genoms from *T. dicoccum* and the C genom (or D = dinkel) from an extinct or yet undiscovered form in Afghanistan or Iran. As existing AABB plants are rust-resistant, lack of resistance in AABBCC plants must be due to the C genom. CC plants may be extinct as a result of low resistance, but if extant must possess some rust-resistant character which could be utilized in breeding for rust immunity. Tetraploid *Aegilops cylindrica* has the C genom, and Johnson (175) found this species highly resistant to some races of rust. Pathak (388), after a study of chromosome morphology, proposed the idea that *T. vulgare* is a hybrid between the diploid *Ae. squarrosa* and a tetraploid form of *Triticum*, the latter having previously arisen as a *Triticum-Aegilops* hybrid. *Ae. squarrosa* has hollow stem and low rust resistance, and it is further suggested that it may also be one of the parents of the tetraploids *Ae. cylindrica* and *Ae. crassa* with which it occurs in Turkistan. It is needless to comment that the origin of hexaploid wheats is still an unsolved enigma and anybody's guess.

That close interrelationships exist among certain species of *Agropyron*, *Triticum* and *Aegilops* is evident (116, 564). The apparent autosyndesis of X_1 with X_2 *A. elongatum* chromosomes in the F_1 meiosis of *T. vulgare* \times *A. elongatum* has led Vakar (548) to suggest that *A. elongatum* is an amphidiploid hybrid, $A_aA_aB_aB_aC_aC_aX_1X_1X_2X_2$, between a tetraploid with the genom formula $B_aB_aX_2X_2$ and a hexaploid with the genom formula $A_aA_aC_aC_aX_1X_1$ such as *A. intermedium*. Peto (400), though apparently studying other races of the *Agropyron* species, also came to the conclusion that *A. elongatum* is an amphidiploid that possibly arose through hybridization of an *intermedium*- (syn. *glaucum*) like plant, AAXXYY, with a 28-chromosome *Agropyron*, XXYY, and the subsequent doubling of the F_1 genoms AXXYY to produce the 70-chromosome amphidiploid.

Haynaldia villosa and species of *Secale* stand apart in that their genoms V and S, respectively, have no counterpart in intergeneric crosses thus far studied (235, 238-242, 267).

Idiograms of *Avena* suggested a close relationship between diploid and tetraploid species (464). *A. barbata* appeared to have two very similar genomes, differing only as to one chromosome, and is probably autotetraploid and derived from a diploid which may also have been a progenitor of *A. strigosa*. The hexaploid oats *A. sativa* and *A. fatua* seemed to have only 18 pairs of chromosomes in common with respect to morphological likeness, but the morphological dissimilarity of the remaining three did not prevent pairing. The hexaploid oats thus far studied differ from the diploid and tetraploid in possessing a larger number of heterobrachial chromosomes.

Haga (154) points out in regard to the stability and mutability of the genom that certain differentiations as a whole of the subgenomes of an allopolyploid lead eventually to a new composite genom functionally diploid and no longer divisible into ancestral genomes though still polyploid as to chromosome number.

More recent discussions concerning the origin, interrelationships or geographical distribution of cereals are available as to 28-chromosome wheats (48), including *T. Timopheevi* (114); the 42-chromosome wheats (105, 106, 140, 141, 293, 446); *Agropyron* (387, 564); *Secale* (275, 446); *Hordeum* (395, 446); *Aegilops* (218, 220, 223); and *Avena* (76, 111, 341).

ANEUPLOID AND STRUCTURAL CHROMOSOME ABERRATIONS

Aneuploidy frequently accompanies directly changes in euploidy, auto- or allo-, but is due also to other factors that disturb the chromosome balance, whether these factors are of natural origin and apparently remote, or induced and immediate. The aneuploidy may be temporary or more or less permanent.

Secale cereale

Some races of *Secale cereale* have a strong tendency to shift from the basic chromosome number seven to eight. Sometimes these 16-chromosome races present further aberrations, as fragmentation and asynapsis (118). Müntzing (357), in a study of 167 rye individuals, found that 69 showed some form of meiotic irregularity. Two plants were trisomic for a SAT-chromosome, and one plant had an additional pair of chromosomes. In a dwarf 15-chromosome plant the trisomic state supposed to have arisen through non-

disjunction also apparently involved the SAT-chromosome (518). At diakinesis usually half of ♂ sporocytes had six bivalents and one trivalent, and the other half had seven bivalents and one univalent. A plant with two fragments of chromosomes (355) gave rise to plants without any fragments or up to eight of them. The increase in number of fragments had a depressive effect on the plant, expressed chiefly by lowered fertility. The fragments were apparently subinert. A plant with one fragment (356) gave rise to plants with new types of fragments which were believed to have arisen through misdivision of the centromere of the fragment, thus forming telocentric chromosomes which in turn through misdivision of the centromere developed into iso-chromosomes. More recently Müntzing (356a), while studying intravarietal crosses involving plants with standard chromosome fragments, has concluded that there may be an old and widely distributed standard type of extra chromosome in rye, and that the deviating types of fragments sometimes observed are more or less ephemeral deviations from the standard. A striking property of the standard fragment in material studied was its ability to increase numerically by non-disjunction at some post-meiotic stage. Experiments strongly indicated that the process of non-disjunction is directed in such manner as to generally pass the fragments to the ♂ and ♀ gametes. The tendency of the directed post-meiotic non-disjunction to increase the number of fragments in the offspring is counteracted by the meiotic tendency to eliminate the fragments. In the Östgöta Gråråg variety the negative effect of meiosis coupled with lowered fertility of plants with fragments seemed to be greater than the positive effect of post-meiotic non-disjunction. In the Vasa II variety, on the other hand, good pairing at meiosis, due probably to genotypical control, seemed to favor fragment increase in the offspring. In Östgöta Gråråg the large iso-fragment derived from the long arm of the standard fragment exhibited post-meiotic non-disjunction, but the small iso-fragment derived from the short arm of the standard did not.

Inbreeding in rye appeared generally to favor various forms of chromosome aberrations (183, 204, 276, 426) exemplified by low chiasma frequency and presence of univalents, chromosome bridges and altered chromosomes. Kakhidze (183) observed that inbred individuals of "Vjatka" rye varied widely as to number of chiasmata and other meiotic characteristics. Homology of chromosomes of

diploid genoms should increase with inbreeding. However, as the accumulation of genes in a homozygous state may cause depression or stimulation exhibited phenotypically in changed fertility, *etc.*, the genic constitution should likewise be reflected in meiosis. The existence of genes causing variations in number of chiasmata and consequently irregular chromosome distribution would through inbreeding isolate individuals differing from one another in the process of meiosis. The general depressive effects of inbreeding would also probably be a contributing factor in rye.

Camara (70) observed that subjection of plants to high temperature of 35°–45° C. greatly increased the inherent instability of rye, and as heat of this magnitude arises in nature it may be responsible for the production of 16-chromosome rye. Popoff (422) attributed extra chromosomes in Bulgarian rye populations to spontaneous crossing with *Secale montanum*. Kostoff (245, 269) found trisomics in the progeny of *Secale cereale* × *S. montanum*, and also one plant with nine normal-sized chromosomes in addition to the expected 14. As *S. montanum* does not grow wild in Sweden, Müntzing (355) concluded that Popoff's theory probably does not apply to aneuploids found in the Swedish rye populations, and is more inclined to believe that fragments are one of several symptoms of cytological unbalance characteristic of *S. cereale*, and possibly other allogamous species. Races with 16 chromosomes disappear, but are frequently reproduced anew by fragmentation and other structural and numerical chromosome aberrations.

Speltoids, Compactoids and Fatuoids

Huskins and Smith (164) attribute the normal head type of *Triticum vulgare* to a balance between ear-lengthening and speltoid glume factors, of unknown chromosome location, and the ear-compacting and round glume factors borne on the long arm of the C-chromosome. In some cases the unbalance may be the result of the mutation of a gene (544). In other cases it is ascribed to numerical or other quantitative deficiencies or duplications in the head-type-determining chromosome in one or more of the three genoms. Uchikawa (545–547) has proposed formulae for various types of speltoids and compactoids studied by him. The off-type heads were frequently accompanied by aberrant chromosome numbers (65, 66, 201, 322, 545–547, 559), but sometimes by deficiency

or duplication in a portion of one or more of the chromosomes concerned (69, 300, 544). Sears (457), in his intensive study of nullisomics, identified the speltoid-suppressing chromosomes as one of the 14 homologous with the 14 in the $1n$ complement of *T. durum* and designated it as IX in his series. Nullisomic IX was hence a homozygous speltoid. The chromosome, the loss of which results in speltoidy, apparently in this case belonged to genomes A or B. Matsumura (322), in a study of pairing in hybrids, has reached a similar conclusion in regard to another nullisomic speltoid. Love (300) found 42-chromosome speltoids with a slightly deficient heteromorphic pair in the progeny of a varietal cross. He believes that deficiencies of this type are likely to occur in hybrids due to breakage at the attachment region in unpaired chromosomes, and to fragmentation due to cross-over in inverted segments. Some of the 42-chromosome speltoids (A series) may have deficiencies too small to be detected cytologically. Camara (69), in the progeny of a pentaploid cross, also found speltoidy associated with a heteromorphic pair. He believes that translocation is the primary cause of speltoidy and that the loss or addition of chromosomes is secondary; the more frequent occurrence of speltoids in northern countries with low temperature may support this theory. Ellerton (105) suggests that the frequent formation of a quadrivalent in the F_1 of *T. sphaerococcum* \times *T. vulgare* may be the result of a reciprocal translocation which involved a chromosome associated with the speltoid character, and that this translocation is responsible for a proportion of heterozygous speltoid mutants in F_2 . Also, as all the *sphaerococcum* characters in the above cross behaved like one recessive gene, Ellerton proposed the theory that *T. sphaerococcum* itself arose as the results of a chromosomal deletion in the population of *T. vulgare* forms which spread into northwestern India from Afghanistan.

Speltoids in *T. vulgare* have their counterpart in fatuoids characterized by wild-oat type of "grain" in cultivated *Avena sativa*. Sander (440) has explained the rise of these aberrants in *A. sativa* as follows: "Alterations in the normal balance between the C chromosome and the rest of the complex give rise to fatuoid, steriloid, and sub-fatuoid mutations. These changes are produced by deficiencies of various degrees in the C chromosome and behave genetically as multiple allelomorphs". Thus removal of the wild-

type inhibitors through loss of all or part of the long arm of the C-chromosome (163) permitted the expression of steriloid, fatuoid or sub-fatuoid characters in varieties of *A. sativa* and *A. byzantina*. Nishiyama (374), in a study of four *Avena* "grain" types, cultivated, intermediate, wild and naked, found that the loss of a pair of C-chromosomes, whether lost from the cultivated, intermediate or wild types, resulted in each case in the wild type. He suggested that in the cultivated *Avena* type the C-chromosome is associated with the cultivated type of "grain" characters, and a B-chromosome is associated with the wild type. In the wild type both the B- and C-chromosome carry the wild type of "grain" factors. In the intermediate type the C-chromosome carries a gene group for intermediate instead of cultivated factors. Experiments indicated that the gene or gene group for naked grain is also associated with the B-chromosome.

Monosomics, Nullisomics and Polysomics

Monosomics ($2n-1$) in which one chromosome of a pair is missing, and nullisomics ($2n-2$) in which both members of a pair are missing, rarely, if ever, exist as diploids. In a polyploid such deficiencies may have depressive effects expressed by reduced vigor or fertility, etc.

Sears (450) obtained monosomics by pollinating a haploid of the hexaploid *T. vulgare* with "diploid" pollen, and nullisomics by selfing the aberrants. Thus 17 of the 21 possible nullisomics have been produced (457). Eleven of the found nullisomics (I-IX) involve the A and B genomes, and six (XV-XX) involve the C genom. All are reduced in vigor, but none is completely sterile. Nullisomic III caused asynapsis and thus provided an additional source of monosomics. Several genetic factors of *T. vulgare* have been located as to their respective chromosomes (455, 457) through this study.

Some monosomics are characterized by various degrees of aberrancy in head (65, 322, 545, 546) and "grain" types (371, 374). In the monosomic offspring of *Avena sativa gigantea* \times *A. fatua* (408) the structurally changed and missing chromosome dominantly controlled leaf width, with the result that the nullisomics had narrow leaves.

Polysomics, in which one or more chromosomes appear in tripli-

cate or higher multiple, may, in contrast to numerical deficiency, occur also in diploids. Trisomic plants in the diploid barley showed at meiosis misdivision of chromosomes of the trisome, and other irregularities (500). In a 15-chromosome sterility group of barley the gametes with the extra chromosome were usually sterile (205).

Sears (450, 457) obtained trisomics directly in the progeny of a haploid *Triticum vulgare* ($1n = 21$), and from a nullisomic (nulli-III) pollinated with the diploid. Tetrasomics arose in the progeny of trisomics with about the same frequency that nullisomics occurred in progeny of monosomics, namely 1% to 10%. It seemed, however, that chromosome duplications were transmitted through fewer ♀ gametes and more ♂ gametes than were deficiencies. Tetrasomics frequently formed quadrivalents, but otherwise meiosis was fairly regular. In the progeny of six tetrasomic plants of different origin, 36 of 44 were tetrasomic. Most of the trisomic and tetrasomic plants were more like the 42-chromosome plants than were the plants with deficiencies. Tetrasomics sometimes compensated in part for nullisomics. Polysomics, like deficiencies, may involve the chromosomes that govern head types (66, 201, 545).

Other Structural Chromosome Aberrations

Observations on chromosome morphology and meiotic chromosome behavior, especially in numerical aberrants, leave little doubt as to the magnitude of the part played by structural aberrations in chromosomes. Camara and Coutinho (74), in a study of eight tetraploid wheats, found considerable variation in chromosome idiograms from species to species. The similarity or dissimilarity did not always coincide with genetical results. They concluded that tetraploid wheats may differentiate subspecies by chromosomal rearrangement, brought about through inversions which would originate deletions, duplications and translocations; by point mutations; or by crossing-over between partially homologous regions. According to Love (300), most and possibly all hybrids between *vulgare* wheats are heterozygous for one or more inversions. In fact there were indications that all varieties of tetraploid and hexaploid wheats used (302) differed to a greater or lesser degree in arrangement of chromosome segments, thus presenting favorable conditions for deletions and other structural chromosome changes. Müntzing (357) found in rye populations plants heterozygous for small inversions as well as for segmental interchanges.

Autopolyploidy accounts for trivalents and higher multiples in some cases, but many others are apparently the result of structural changes in one or more of the chromosomes involved (88, 302, 404, 450, 451, 489, 496, 499, 500, 525, 527). Crossing-over in more or less dissimilar chromosomes (197, 228, 244, 302, 370, 372, 408, 451) in auto- or allosyndesis no doubt figure in these structural chromosome changes. Kostoff (246) suggested that the comparatively dense heterochromatin at the ends of chromatids may be responsible for end to end pairing in haploids and in certain cases may lead to chiasma formation. The association of heterochromatic portions of non-homologous chromosomes in hybrids might lead to interchanges and production of forms with reorganized karyotypes. In haploid *Secale cereale* heterochromatin ends apparently played a part in pachytene pairing of non-homologous chromosomes (285). Frequency of sporocytes with multiple chromosome associations in different pentaploid wheat hybrids varied from less than 3% in Hope \times Vernal, to more than 90% in Marquis \times Pentad (302). The suggestion was offered that the multiple associations arose through pairing of chromosomes which were phylogenetically similar but not strictly homologous. Telokinetic chromosomes (189, 302, 304, 356, 457) resulting from loss of one arm through misdivision of the centromere (189) may give rise through a second misdivision to isochromosomes with two identical arms. Sears (457) obtained a telocentric or an isochromosome or both from 15 of the 17 identified chromosomes of *T. vulgare*, most frequently in the offspring of some monosomic individuals. Univalent chromosomes resulting from hybridization in wheat were found to be a fruitful source of telokinetic chromosomes (302, 304). As a result of breaks at the kinetochore one or both arms might bear a spindle attachment and participate in the subsequent nuclear divisions. Terminal kinetochores were, however, usually unstable.

Altered chromosomes of more unusual types sometimes occur (204, 426). A chromosome in which a peculiarly shaped end appeared to function in some ways as a centromere was discovered in rye (426).

Fragmentation, a common phenomenon associated with other structural chromosome disturbances, has been observed in amplified forms in certain mutations (498).

ASYNAPSIS, DESYNAPSIS OR DISSOCIATION

Asynapsis is characteristic of meiosis in many F_1 hybrids and progenies where low homology and structural differences interfere with chromosome pairing. There are other cases where conditions are seemingly amenable to bivalent formation yet univalents are abundant at first metaphase. The chromosomes may be paired at middle prophase but fall apart before the entry of the chromosomes on the spindle. The terms desynapsis and dissociation may better describe these latter types of asynapsis.

A strain of rye showed pachytene pairing, but by metaphase many of the pairs had dissociated in both ♂ and ♀ sporocytes (425). The dissociation was controlled by a single recessive factor. An apparently spontaneous mutation in F_3 of a varietal cross in a hexaploid wheat was characterized by a high state of asynapsis at first metaphase with the number of pairs, mostly of the end to end type, varying from zero to 21 (289). Normal prophase pairing occurred in all the plants, but in some of them desynapsis began at pachytene and in others at diplotene. The aberration was a simple Mendelian recessive character. There were, possibly, modifying genes present. Fertility was lowered in varying degrees. Other dissociation mutants appeared in the progeny of interspecific hybridization and as result of X-ray treatments in diploid wheats (495-498). A nullisomic of *T. vulgare* was partially asynaptic (nulli-III) (457). Factors affecting synapsis in oats were located in the C-chromosome (163), which also in part controls "grain" types.

The delicate balance in both unstable and stable pairing may be disturbed by external conditions. Li, Pao and Li (289) found the gene governing desynapsis most effective at low temperatures approaching 10°C ., and only then was desynapsis complete. Prakken (425) ascribed an increased frequency of univalents in an asynaptic rye during one season to high temperature and low water content in soil and air. Fixations on different dates showed that environment influenced significantly the meiotic instability in varieties of common wheat (360). Inbreeding in rye favored lower chiasma frequency and increase in number of univalents (276). Bondarenko (53), in surveying the fertility of *Triticum-Agropyron* hybrids, concluded that all life processes in the organism and especially chromosome conjugation are dependent upon environmental conditions.

STERILITY

Gamete and seed sterility may at least in part be attributed to chromosome aberration in some form. Hybrid sterility in general has been ably reviewed by Thompson (522).

Defective pollen tube growth may be an immediate cause of pollen sterility, and is apparently a contributory cause of self-sterility in rye (448). Matsumura (323, 327) observed that pollen of *Triticum spelta* ($2n = 42$) germinated far better than pollen of *T. polonicum* ($2n = 28$) on the stigmas of *T. polonicum*, *T. spelta* and the F_1 hybrids of the two. The pollen of the hybrid germinated very poorly.

Histological studies have revealed that failure to obtain hybrids between apparently incompatible species may not be due to failure of fertilization. In *Triticum-Elymus* hybridization experiments fertilization took place, but the embryo and endosperm either failed at the beginning or developed through the earlier stages and then aborted (413). Failure in *Hordeum* \times *Secale* was due to early death of embryos following abnormal development of the endosperm and its degeneration after five or six days (61-63, 91, 523). The most striking feature of the endosperm development was the failure of nuclear division to keep pace with chromosome division, thus increasing the polyploidy of each of the few nuclei formed to 100 or more chromosomes and one to 20 nucleoli (526). Among suggestions offered as to causes of endosperm and embryo degeneration (526) are that some kind of immunity reaction may take place between ♀ plant and hybrid tissue, or that ♀ plant may not produce the right kind or right amount of food for the hybrid with a different genetic constitution. Pissarev and Vinogradova (411) were able to obtain *Triticum-Elymus* hybrids beyond the embryonic stage only when each parent plant had developed from an embryo transplanted onto endosperm of the respective foreign genus. The spring wheat *Lutescens* 62 in hybridization with rye gave 25% success when grown from embryos grafted upon rye endosperm, but only 4.3% when grown from ungrafted embryos.

Success in obtaining hybrids between plants of unlike chromosome numbers frequently depends on the direction of the cross. The autotetraploid *Secale cereale* ($4n = 28$) ♀ \times *S. cereale* ($2n = 14$) ♂ set seed, but the reciprocal was unsuccessful due to failure of pollen tube growth (85). In *Hordeum* ♀ \times *Secale* ♂ the embryo

developed to a certain stage, then failed to develop further (526). In the reciprocal even inception of endosperm and embryo failed. Auto-"triploid" *Triticum vulgare* (42+21) ♀ × *T. vulgare* (2n = 42) ♂ produced a grain set of 68.8%, but the reciprocal was sterile (569).

The grain set may be good but the germination a failure. Pentaploid grains were produced more freely when the tetraploid wheat was the ♀ parent, but grain viability was poor. The reciprocal with the hexaploid wheat as the ♀ parent produced fewer but viable grains (50, 55, 462, 522). Similarly the direction of the cross conditioned the hybridizing results obtained in a triploid *Avena* hybrid (368); in *T. vulgare* (2n = 42) × *Secale cereale* (2n = 14) (55, 522); also in back-crossing of pentaploid wheat hybrids to their tetraploid and hexaploid parents (319), and octoploid *Aegilotriticum* to its tetraploid components (193).

The immediate cause of embryo inviability, in whatever stage of development, of low-chromosome ♀ × high-chromosome ♂, it seems, is the abnormal development of the endosperm (55, 368). The primary causes apparently lie with unfavorable relationships as to chromosome numbers in embryo, endosperm and maternal tissue. In contrast to the above results, *Triticum-Agropyron* hybrids were obtained with greater ease when self-pollinating *Triticum* served as the ♀ parent, irrespective of chromosome numbers (34, 211, 279). Only *A. elongatum* among the *Agropyron* species crossed with *Triticum* was found to be self-pollinating, and then only partially so (494).

Crossability in general is often greatly influenced by varieties (493). In crosses with *T. Timopheevi* grain set varied from zero in one strain of *T. spelta* to 93% in one strain of *T. compactum* (521). *Triticale* (Rimpau) ♀ × *Secale cereale* ♂ gave no grain set, but its substitution by *Triticale* (Meister) ♀ gave 23% (284). Fortunate choice of parental strains augmented grain set from 10% or less to 90% or more in crosses between *Triticum* and *Agropyron* (561). Race was found to affect success of the tetraploid *Triticum-Secale* crosses (98, 558). Rye pollen gave germination of 10% and 60%, respectively, on stigmas of two varieties of common wheat, Marquis and Chinese (55).

For some of the cases of sterility definite genetic bases have been discovered. When crossed with Petkus rye Marquis wheat ♀ pro-

duced less than 3% grain set, while Chinese wheat 466 ♀ produced 60% or more. Marquis ♂ gave no grain set, but Chinese 466 ♂ gave 2.2% grain set with 50% germination. Lein (283) attributed the crossability of Chinese 466 to two genes designated as kr_1 and kr_2 . Male sterility in the form of shrunken rudimentary anthers, in a *Hordeum* mutant, was found to be a recessive factor segregating three normal to one ♂ sterile (514, 515). Bagged ♂ sterile plants were completely sterile, open-pollinated highly fertile. Another sterile form of *Hordeum* (205) bore a gene, carried by the pollen, that disturbed the embryo sac development, possibly by interfering with the antipodal tissue formation. Varieties of *Triticum monococcum* were observed to possess genes which were dominantly lethal when introduced into a cross with *Aegilops umbellulata*, causing the death of the hybrid embryo (452, 456). *T. aegilopoides*, a species closely related to *T. monococcum*, did not carry these genes, and neither did some of the segregates from *T. monococcum* × *T. aegilopoides*.

The self sterility of *Secale* may in part be attributed to weak pollen-tube growth caused by an inhibitory substance produced by the ovary (448). This substance exerted the strongest influence in the lower style where germination was frequently prevented. However, as pollen tubes sometimes entered the embryo sac but without subsequent grain development (278), other factors also were apparently responsible for the sterility and were further aggravated by self-fertilization. Müntzing (348) found that pollen sterility in varying degrees was common in rye populations and was inherited. About half of 610 plants examined could be classed as partially ♂ sterile. Ovular sterility correlated weakly with pollen sterility. Landes (278) conceded that weak pollen-tube growth in selfed *Secale* was in part the cause of sterility, but found also that 5%–10% of ovaries examined had no embryo sac. Twice as many embryo sacs aborted in the selfed as in the cross-pollinated florets.

Aneuploidy may in some instances cause sterility. In trisomic *Hordeum* eight-chromosome gametes were usually sterile (205). Poor or shrivelled grains of autotetraploid *Secale* were more frequently associated with aneuploid embryos than were plump grains (354). Hypotetraploid embryos favored shrivelling more than hypertetraploid. Similar correlations were observed in the diploid and aneuploid progeny of triploids, and may in general be due to

disturbed balance of chromosome numbers in respect to embryo, endosperm and surrounding tissue.

Certain structural chromosome changes frequently influence fertility, due to mechanical disturbance of meiosis. Reciprocal translocations following X-rays and intercrossing of progeny in *Triticum monococcum* were found to lower fertility (497, 499). A ring of six chromosomes produced an average sterility of 31%, a ring of eight chromosomes 51%, a ring of ten chromosomes 66%, two rings of four chromosomes 24%, and one ring of six together with a ring of four chromosomes 48%. No ring resulted in only 5.5% sterility. In 4,200 cells 73% had rings arranged in a zigzag manner. This disjunctional division of chromosome complexes reduced the sterility materially below that expected for random segregation (499, 525).

Meiosis in *T. Timopheevi* ($2n = 28$) \times *T. armeniacum* ($2n = 28$) was remarkably regular and tetrads were apparently regular, but most of the pollen was entirely deformed (516). It was thought that pollen sterility might have resulted in this case because the chromosomes of one species could not be substituted for those of another, due to divergences in the parental forms developed through gene mutations and structural chromosome changes.

External conditions may also temporarily influence fertility. *T. durum* \times *T. Timopheevi*, sterile under ordinary field conditions, was under high soil fertility induced to produce some grains (579, 580). However, even under favorable cultural conditions the undoubled *Triticum Timopheevi* \times *T. durum* remained highly sterile compared with the corresponding amphidiploid (588). Excellent nutrition apparently cannot overcome the cytogenetical causes of sterility. Use of pollen from later-generation offspring, and to a lesser extent the artificial breaking of the F_1 anthers, favored increased fertility in the above F_1 hybrid (580). X-rayed pistils of *T. spelta* produced approximately 20% grain set when pollinated with *T. Timopheevi*, whereas the control was negative (520). It was suggested that the X-rays had weakened the inhibitory action of the hexaploid stigma toward the diploid pollen. Sterility of varieties of wheat, grown under adverse conditions of northern Caucasus and regions within the arctic circle, was ascribed to failure of fertilization of the polar nuclei (28). These nuclei were much elongated and densely surrounded by cytoplasm.

POLYPLOIDOGENIC, ETC., AGENCIES

Chemicals

The most extensively used polyploidogenic chemical since its widespread introduction in 1937 (156) is colchicine derived chiefly from *Colchicum autumnale*. In U.S.S.R. alone, during a brief period, more than 90 new amphidiploid wheat types have been produced by means of colchicine treatment (594). The effect of colchicine on the cell dynamics has been described by Beams and King (42), Derman (96) and Beal (41), and its chemical nature by Shmuck (469). Some aspects of the molecular structure of colchicine distinguish it sharply from other alkaloids, and at the same time approximate it to another group of substances, the sex hormones, and the carcinogenic hydrocarbons (469). Some of the histological features induced by colchicine present an analogy to those found in cancerous animal tissues and some plant galls and tumors (156, 252, 469).

In cereals colchicine has been applied usually in concentrations of 0.05–0.5% in aqueous solutions to dry, or to water-soaked and germinating grains (42, 57, 78, 119, 145, 188, 252, 325, 342, 409, 449, 461, 584, 586), usually for 24 to 48 hours. It has also been injected into coleoptiles (64, 392) and applied to crowns of plants (453) or florets (325). In a mixture with lanolin it has been employed in salve form (453). Pulp of *Colchicum* employed as a germinating medium produced doubling of chromosomes of wheat and rye (259).

The colchicine treatments have resulted in highly varying degrees of success. The balance between polyploidogenic and lethal effects is delicate. Outstanding success was achieved by Greis (145) who obtained 14 tetraploids and 18 chimeras from 100 treated barley seeds. The best concentration was 0.4% for 48 hours on grains in early stages of germination. Excellent results were also attained by Sears (453) by treating eight to 11 mm. long coleoptiles of diploid F_1 hybrids with 2% by weight of colchicine powder in anhydrous lanolin for 24 hours before planting in soil. Another highly successful procedure was to apply to crowns of potted plants, before jointing, cotton saturated twice daily with 0.5% aqueous colchicine solution for four or five days. This method was advantageous in rare hybrids in that the plant could be divided so as to increase the number of individuals. The treated plants were usually

chimeras with only some heads or parts of heads polyploid to furnish seed for the completely polyploid generation.

Apiol (132-134) and its isomers extracted from parsley, *Petroselinum crispum* (syn. *Apium petroselinum*), brought about anomalies similar to those produced by *Colchicum*. Parsley contained sufficient polyploidogenic substances to produce tumors, and increased polyploidy in wheat grains germinating in its vicinity (132).

Convallarin, a glucoside derived from *Convallaria*, in 0.5% and 0.8% aqueous solutions produced on root tips of wheat seedlings small tumors of multinucleate cells but no polyploid nuclei (5).

Of the artificially synthesized chemicals acenaphthene has been tested most widely (136, 207, 247, 250-253, 365, 469, 470, 486). The general morphological hypertrophies and cytological aberrations were similar to those produced by colchicine. The solubility in water is only about 0.003%, and hence the crystals may be scattered over the moist plant organs without danger of too high dosage. Acenaphthene is less expensive and less toxic than colchicine and has shown indications of being more selective in its effect as to plant species. Growth was inhibited by its application in wheat, but not in peas, beans or lentils (172). *Colchicum autumnale*, unaffected by its own polyploidogenic substance, colchicine, responds to acenaphthene with disturbed mitosis and increased polyploidy (207).

Many other chemicals have been tested as to polyploidogenic properties. Shmuck and Gusseva (471) have synthesized more than 100 different carbocyclic and heterocyclic substances. The chemicals are presented with structural formulae and tabulated to show their respective biological effect on wheat, and their analogy to the respective carcinogenic substances. Some of the compounds affected alike all plants tested; others affected one group and not another. The cereals, wheat and barley, were highly responsive; the legumes, peas, vetch, and clover, least so. The chemical nature and biological effect of synthetic substances are further discussed by the above (472-477) and other authors (117, 130, 131, 135, 137, 138, 282, 482, 483, 485-487).

One small group of chemicals, certain mercuric compounds, deserve mention, as they are active ingredients of some fungicides. "Ceresan" contains ethyl mercury phosphate and caused hypertrophy in oat and other seedlings when used in aqueous suspension

of 1:2000 (444). "Granosan" contains 2% of ethyl mercury chloride and when used in aqueous concentrations of 0.5–0.1% (equal to 0.01–0.002% ethyl mercury chloride) for three to six days caused the usual polyploidogenic results in cereals (260, 264, 447). "Niuifa", another mercuric seed disinfectant, produced similar results (447).

X-rays

X-ray irradiation as a polyploidogenic agency is apparently more effective at lower dosages of 250 to 500 r (2, 3). With 1,000 r and upward the frequency of polyploid cells in rye decreased (59, 60). Among 533 rye seedlings X-rayed at 250 r for the express purpose of obtaining polyploids, two developed into tetraploid plants and other individuals had polyploid sectors (56). In root tips of *T. monococcum* also haploid cells and sectors were observed (67).

In cereals X-rays have usually been applied to air-dried grains or to seedlings. At low dosages of 250 to 500 r, the number of mitotic cells in rye increased greatly with a subsequent increase in yield (58–60). Following dosages of 1,000 r or more, chromatin abnormalities increased, and rate of mitosis and final grain yield decreased. Exposure of air-dried grains of *Triticum durum* to 16,000 r reduced the frequency of cell division 42% (6), and markedly retarded growth. Exposure of wheat spikes to 16,000 r produced nuclear disturbances in about one third of the florets (8). The resulting pollen grains were of diverse sizes and chromosome numbers, and the grain yield was reduced. Sterility of ovaries in barley was greater when X-rays were applied to heads immediately before flowering than when applied at earlier phases of plant development (410).

The X-ray effect was persistent, as X-rayed dormant grains of *T. vulgare* stored several months to three years before being allowed to germinate showed no decrease in the cytological irregularities induced by irradiation (4, 7).

Certain factors have been found to influence the effect of X-ray irradiation. Covered grains of barley and oats, after dosages of 10,000, 15,000 and 20,000 r, gave a markedly higher germination percentage than hulless grains (128). Larger grains with correspondingly larger embryos in two varieties of wheat survived 20,000 r with less mortality than smaller grains. Higher water content of grains, affecting their metabolic activity, increased mor-

tality at higher dosages (127, 139, 150). Associated with the lethality were meiotic disturbances. At 10,000 r grains of barley containing 10% of water showed 12.66% of mitotic disturbances in germinating embryos; 15% of water, 27.99%; and grains soaked 23 hours, 53.8% (139). The percentage of nuclear aberrations in barley increased also with each added year of storage of grain before X-ray irradiation (151, 152).

As referred to in the discussion of autopolyploids (350, 353, 503), tolerance to X-rays in general increases with degree of polyploidy. Marshak and Bradley (308) noted that the degree of inhibition of mitosis in wheat seedlings was inversely proportional to chromosome number. It was neither inversely nor directly proportional to the aggregate chromosome length of the chromosome complement, which in the hexaploid nucleus was almost twice that of the diploid nucleus instead of three times as should be expected on the basis of genom number. There was evidence to indicate that the inhibitory action of X-rays on mitosis might take place through the centromeres. The importance of the centromere in the initiation of mitosis is indicated by the behavior of micronuclei during mitosis. Micronuclei retain structural integrity until the major nucleus of the cell enters prophase. Simultaneously with the major nucleus the micronuclei go through the characteristic changes if their chromosomal components contain centromeres, if not they become pycnotic and disintegrate. The theory was proposed that radiation will reduce the number of mitosis-initiating centers, which may possibly be identified with centromeres, in proportion to the number present in the cell. Thus if one half of the centromeres are inactivated, seven should still be intact in the diploid, 14 in the tetraploid, *etc.*, and inactivation of a sufficient number of centers to cause mitotic inhibition would require a heavier dosage in the tetraploid.

X-ray-induced chromosome abnormalities, unlike X-ray-induced mitotic inhibition, increased with the degree of polyploidy. The number of chromatic bridges (503) in root-tip mitosis of wheat seedlings following exposure to 10,000 r increased with each rise in genom number from an average of 0.7 per cell in diploids to 1.7 in tetraploids and 2.2 in hexaploids. Likewise the frequency of translocation rings resulting from fertilization of wheat florets with X-rayed pollen rose with each succeeding higher degree of poly-

ploidy. Fröier, Gelin, Gustafsson and Tedin (126, 129) found that at 5,000 r the number of disturbed nuclei in seedling roots of X-rayed wheat grains was directly proportional to the degree of polyploidy. At 15,000 r, however, the amount of nuclear disturbance had risen more rapidly in the diploid than in the hexaploid. The seeming discrepancy might be explained by the discovery by Marshak and Bradley (308) that the total chromosome length per genom was considerably less in the hexaploid than in the diploid, and also by the general observation in various plants and animals that the frequency of X-ray-induced chromosome abnormalities varies directly as the total length of the chromonemata of the somatic chromosome complement.

The germinating and sprouting ability of the hexaploids remained unaffected even when more than every second mitosis was disturbed (126). In the diploid *T. monococcum* there was a pronounced decrease in growth, even with few nuclear disturbances and low X-ray dosages.

A Mendelian factor in *T. monococcum* increased the susceptibility of dormant seeds to X-ray injury (501), but seemed to have no effect on mutation rate.

Among the various forms of X-ray-induced nuclear disturbances some involved specifically chromosome aberrations, numerical as well as structural, including fragmentation, inversions, bridges, translocations, *etc.* (67, 139, 151, 503).

Camara (71, 72), in a study of two pairs of SAT-chromosomes in *T. monococcum*, concluded that the two regions of most frequent breaks were one near the centromere and the other near the distal end. The region near the centromere also had a higher power of fusion. SAT-1 chromosome was less resistant to X-rays than SAT-2 chromosome.

X-ray irradiation has been a profitable method of obtaining mutations. Some of the mutations conspicuously affected meiosis in form of extensive chromosome fragmentation, partial or complete asynapsis at metaphase, diploid spores and chromosomal rings (441, 495, 498). Other mutations included abortion of anthers before or after meiosis (498); shortening of growth period, thus allowing growth of more than one generation per year (410, 496, 498); change from spring to winter habit (306); high resistance to *Erysiphe* (123); chlorophyll deficiencies (150, 152, 153, 178, 353,

410, 495, 498); dwarfs (178, 410); fatuoids (95); tubular heads (410; speltoids, *etc.* (441, 495, 498). Factors as biotypes (441), water content of grain (152) and age of grain were sometimes effective in determining the type of mutations obtained.

Temperature

Natural climatic temperatures have been credited with altering the chromosome status in some instances. Garnet wheat grown in Schleswig-Holstein showed 24% of sporocytes with univalents, but only 5.8% when grown in its native Canada (44). Mention has been made of extreme natural temperatures in connection with spontaneous rise of speltoids (69) and haploids (429). Root tips of *Hordeum bulbosum* fixed during cold weather showed a low chiasma frequency and a large number of univalents (45).

Experiments on the effect of temperature on the induction of chromosome aberrations have been limited mainly to heat, including ranges from 35° to 50° C., and in one case of dormant grains a temperature of 80° C. (503). Some treatments involved sudden extreme temperature changes (402, 403). Exposure time varied from 20 to 60 minutes, to several hours or to several days. Heat was applied most frequently to the spikes at some chosen stage between premeiosis and early post-pollination. Grains were treated in dormant stage (503) or allowed to germinate at the high temperatures (399, 401).

Root tips of rye seedlings germinating at 35° to 36° C. showed fractured chromatids, translocation, abnormal chiasma formation, *etc.* (399). Treated heads of rye frequently gave rise to abnormal meiosis including structural chromosome changes (77) and decrease in number of chiasmata to complete asynapsis (70). Kagawa (179) reports diad formation in two heat-treated plants as averaging 3.5% and 8.6%, respectively, as against 0.3 to 1.6% in four controls. Sparsely among the progeny of heat-treated plants there arose "tetraploids" (99, 121, 185, 186, 358, 402, 403), numerical chimeras (68, 181, 186, 401) or haploids (375). Heat alternated with cold resulted in one amphidiploid (402, 403). Tolerance to heat, contrary to the response to X-rays, was not favored by higher chromosome numbers (503).

High temperature that produced a number of mutants in two strains of *T. compactum* produced none in a variety of *T. vulgare*

(181), indicating perhaps differences in reaction between the two species. Low temperature greatly increased the effectiveness of a gene governing desynapsis in a wheat mutant (289). The effect of low temperature in differentiating compound chromomeres and amplifying secondary chromosome constrictions has been briefly referred to under chromosome morphology.

Centrifugal Force

Ultracentrifugal force of 150,000 to 400,000 times gravity in stratifying the cell contents displaced the spindle to the end of the cell (42). The metaphase stage frequently recovered the normal state. The late anaphase stages often suffered permanent disruption as the two nuclear masses were displaced more strongly centrifugally away from the spindle which through displacement or inactivation failed to initiate cell wall formation. The result was often binucleate cells, and sometimes multipolar spindles in the subsequent division.

Centrifuging caused structural chromosome changes in *T. monococcum* (73). Chromosomal breaks occurred more extensively during the first 12 hours following the treatment. Fusion of breaks did not follow immediately. Wheat grains, at point of breaking seed coats, centrifuged for various periods at 3,000 revolutions per minute, lost in survival value with increasing doses (66). Various mutants, including aneuploid speltoids, were obtained.

Miscellaneous Agencies

Germinating seeds of common wheat placed in a tube with both ends attached to electrodes and subjected to electric currents of varying intensity gave rise to some aneuploid speltoids and other mutant plants (65). The rate of mutation tended to increase with exposure, more evidently so when direct current was applied.

Grains of wheat exposed to the light of the spark of an induction coil resulted in mutants characterized in part by higher resistance to lodging and diseases, and by 10 days earlier maturity (115).

Seedling roots of barley immersed in 1:75,000 aqueous solution of neutral red for one hour, then grown in dark, showed mitotic abnormalities as pycnosis, anaphasic bridges and pseudomitosis, not seen in proper controls (391). Cell division ceased after seven hours.

Barley seedlings grown in an oxygen-free atmosphere of nitrogen showed various nuclear abnormalities, as clumping of chromosomes, sticky anaphase bridges and extrusion of chromatic material (511, 512). Seedlings treated four days recovered after a few days in normal air, but a six-day exposure was lethal.

The cytological aberrations associated with extended seed storage have been well summarized by Crocker (94). Aberrations appeared in rye sometimes after only two to three years of storage, and included structural chromosome changes (366). In one lot of eight-year old seed, 43.8% of mutants developed.

EMBRYO SAC, EMBRYO AND ENDOSPERM

During the past decade more cytomorphological studies have been directed toward the development of the embryo and related structures.

The rate of pollen-tube growth is apparently variable with plant race and growth conditions. In rye pollen-tube growth was generally completed within 24 hours after pollination (448). In barley pollen germination began five minutes after reaching the stigma, and in 45 minutes one ♂ gamete was in contact with the egg, the other with the two fused polar nuclei (415). The most rapid pollen-tube growth in barley took place at 30° and 35° C. when the ♂ nuclei were present in embryo sac 20 minutes following pollination (420). At 5° C. the same growth required 140 minutes. The triploid endosperm nucleus showed division figures within six hours and the zygote within 14 hours (415).

The development of embryo sac and early post-fertilization stages have been illustrated in wheat (28, 338), rye (43), normal (331, 397) and sterile (205) plants of barley, and embryo-endosperm relationships in reciprocal crosses involving parents of unlike chromosome numbers (55). In countable stages nuclear division occurred three times as often in the endosperm as in the embryo, and Pope (420) suggested that the extra set of genes in the endosperm may be the major factor in its rapid growth. The optimum temperature for growth seemed to be about 30° C. One hour's exposure to 40° C. brought about signs of injury to egg and polar nuclei.

Antipodal tissue, highly developed in Gramineae, probably functions directly in the early nutrition of the endosperm, and indirectly in the nutrition of the embryo (62, 91, 526).

Plump grains without embryos are found in small numbers in cereals. Some varieties produced very few to none of these sterile grains, others produced up to 3% in some years (148), and the rate of occurrence was also higher in cross-pollinated plants like rye. The immediate cause of embryoless grains is assumed to be single fertilization whereby only the endosperm develops. Hybridity and growth conditions are modifying factors. Single fertilization may also affect the egg, in which case no endosperm forms. Endospermless grains, however, are lost in screening due to their light weight and shrivelled state. Experiments on the inheritance of spontaneous embryolessness in spring wheats did not give conclusive results.

Apomixis, reported in some members of the Gramineae, was observed among perennial segregates of the back-cross (*Secale cereale* \times *S. montanum*) \times *S. cereale* (263). Small leafy plants with rootlets occupied the place of anthers and ovaries in the spikelets, and developed into normal individuals when planted. The apomixis and vivipary in these segregates were induced by low temperatures of 0°–10° C. At temperatures above 15° C. normal sexual reproduction took place. Induced vivipary of normal but immature embryos of barley varieties possessing extreme dormancy was brought about by exposing the embryo end of the ovary to constantly wet filter paper (417, 421).

The feasibility of obtaining viable grain from cut flowering culms stored in water has been demonstrated by Pope (414, 418). The satisfactory storage of ovaries and pollen on cut culms at low temperatures for 21 days or longer may be of distinct advantage in hybridization of forms with unlike ripening dates (416).

It now seems possible that rescue may be in store for some of the many cereal hybrid infants finding conflicting forces too turbulent for a happy existence. Embryos of *Hordeum jubatum* ($2n = 28$) $\varnothing \times$ *Secale cereale* ($2n = 14$) \mathfrak{J} normally died before maturity (61, 63). One of several embryos excised from caryopses and grown in cultural solution, however, developed into a mature plant. Barley embryos of different ages, grown on artificial media, produced small seedling-like plants (331). Cell differentiation was more distinct in the cultured embryos and aided in the interpretation of the development of naturally grown embryos.

Observations were made on the state of chromosomes of oat embryos during dormancy (508) and initial germination (513).

Summary of work on endosperm of Gramineae, to year 1939, has been presented by Alexandrov (11). Alexandrov and Alexandrova have made extensive studies on the endosperm, especially in *Triticum*, including earlier stages of formation (21, 23, 25) and later stages of development (339). They have sought to determine the histological structure and the status of ergastic substances, as starch and protein in relation to flinty and floury endosperms (14, 15), endosperms of soft and hard wheats (22); of full and meager grains (16, 17), and of grains produced by plants with short and long ripening periods (24). As the endosperm matured, the nuclei, especially in the deeper layers, first increased in size, then became deformed, shrank, died and finally disintegrated (19). Formation of small starch grains continued during the nuclear disintegration.

The endosperm of some species of *Agropyron*, as *A. intermedium* and *A. elongatum*, seemed very similar to that of *Triticum*. Both large starch grains of plastid origin and very small grains of chondriosomal origin were present (18). In other species, however, as *A. cristatum*, the chondriosomal starch was absent or very scant, and a calcium oxalate druse apparently replaced the nucleus at maturity.

One characteristic of the high-baking qualities, in contrast to low-baking qualities, of some Russian wheats was the lower amount of chondriosomal starch and higher degree of protein intercalation in the endosperm of the high-baking grain (169). Jakólev (170) observed that in several species of wheat cross-pollination favored the development of less fine-grained starch as well as of a larger proportion of protein. Heads were selfed on one side and emasculated on the other to favor cross-pollination with other individuals of the same variety.

Rudiments of protein grains were detected in oat endosperm 14 or 15 days after pollination (396). One grain appeared in the center of each of numerous, probably proteinic, vacuoles in the cytoplasm of the aleurone cells.

Amylolytic activity and sugar compositions were determined in wheat species of the three chromosome groups (231). The amylolytic activity was lowest in the diploid *T. monococcum*. Maltose contents as well as total sugars were high in tetraploid *T. durum* and *T. polonicum*; low in diploid *T. monococcum*; intermediate in

tetraploid *T. dicoccum* and *persicum*, and in hexaploid *T. vulgare*, *sphaerococcum*, and *spelta*.

Transplanting of embryos to foreign endosperm has been found to reduce grain dormancy (573). Germination was advanced more by transplanting to non-dormant than to dormant grain types. Various morphological and physiological responses have been induced in endosperms in caryopses of plants grown from embryos grafted onto endosperms of other genera (411, 478). The endosperms of grains born by plants of graft origin acquired some of the characteristics of the adopted endosperm, as to pigmentation of grain, quality of gluten, quantitative relationship of starch and protein, etc. It has been suggested that the phytohormone action of the borrowed endosperm might be the main cause of these changes. The transplants were made between dry caryopses, the foreign embryo being cemented into the position of the replaced native embryo with paste made from flour of the same genus as the adopted endosperm (411).

The advantage of large endosperm in spring wheat was demonstrated by increased vigor and yield attained when an extra endosperm was joined to the one already possessed by the embryo (146).

Xenia in small grain cereals (52, 81, 124, 309) is apparently not readily discernible. The phenol color tests, used to distinguish grains of different wheat and barley varieties (233), when applied to grains of wheat crosses produced the same color reaction as grains of the maternal plant (336). The grain from the F_1 plants was colored irrespective of the direction of the cross.

Cyto-histological studies dealing more exclusively with pericarpic structures have been made available by Alexandrov and Alexandrova (10, 12, 13, 19, 20, 26, 27). Varietal differences in the structure of the wheat grain are illustrated by Bates (40).

Flowers with two or three carpels developing into fertile grains have been found in several lines in the progeny of a varietal cross in *T. vulgare* (332). The percentage of flowers with multiple caryopses averaged about 70.5 in earlier generations.

VEGETATIVE GRAFTS

Aside from the grafting of entire embryos onto endosperm, embryonic, as well as hypernodal grafting on young culms, also has been described (165, 412).

MITOTIC PERIODICITY

A study of mitotic periodicity, in root tips of month-old seedlings, indicated primary diurnal periods of high mitotic activity shortly after 12:30 A.M. and 12:30 P.M. in *Hordeum vulgare*, *Triticum vulgare*, and *T. spelta*, and apparently none in *T. monococcum* and *Secale cereale* (437).

SUMMARY

Added study of cereal cytogenetics has further substantiated the apparent fact that with the great powers of stability inherent in the chromosome architecture there are allied equally great forces for numerical and structural changes, implying inevitably genic redistribution. Many of these alterations escape detection under present cytological methods.

Deviating chromosome numbers of spontaneous origin are conspicuously demonstrated in natural species. One source of euploid changes is polyembryony. While on the average some 3,000 cereal grains may be required to produce one set of multiple embryos and nearly 60,000 grains to produce one seedling with an altered chromosome number, these seemingly scant aberrants may become an impressive factor if now and then through the centuries a survival chance occurs. Also, some races produce a much higher number of caryopses with multiple embryos. Outside the phenomenon of polyembryony, too, natural causes bring about euploid aberrancy, operating either through the reproductive mechanism or through vegetative mutation expressed in form of chimeras.

Artificial means of producing chromosome changes have been applied with increasing endeavor. Among polyploidogenic chemicals colchicine has so far produced the most satisfactory results in raising the degree of euploidy. Acenaphthene has been found to be more effective in cereals than in some other plant groups. Reports are available also as to the efficacy of numerous other chemicals, including some well known disinfectants.

Increase in euploidy has sometimes followed extreme temperatures and extreme temperature changes.

While X-rays in higher dosages are very effective in bringing about general mutations, it is subsequent to low dosages that euploid chromosome changes have directly been most frequently observed, either as tissue sectors or entire plants.

Many cereal haploids, spontaneous or induced, have been observed. Though these highly unstable and often less robust replicas of the female parent have no immediate agronomic value, some recent experiments indicate that they may become highly important in the cytogenetic analyses of the species or race, as well as outstanding in demonstrating the instability of chromosomes. "Triploids" also should probably be classed in the category of valuable experimental material.

Some cereal "tetraploids" may become agriculturally important. Morphological and physiological comparisons indicate that some striking differences occur between the "tetraploid" and its parental diploid. The forms and directions that these differences may assume seem to be conditioned by the species and race involved, and probably also by the ecological environment of the individual plants examined.

There are indications that very high euploidy in plants with long chromosomes, as in "small grain" cereals, is unfavorable to plant vigor and survival value.

Hybridization apparently is one immediate cause of numerical chromosome changes. Natural hybrids are reported in cereals and their near relatives. In artificial production of hybrids the main emphasis at present is placed on conversion of sterile and unstable F_1 hybrids into more or less fertile and stable amphidiploids. The number of these auto-allopolyploids is rising so rapidly that a babel of new generic and specific terms is foreseen, unless plant breeders and taxonomists collaborate universally in the naming of the new mongrels and also in the preservation of a few replicas in well regulated herbarial galleries.

The various amphidiploids may be objects of great hope or of equally great doubt as to valuable agronomic prospects. Some show immediate promise; others may have hidden values to be discovered only in the distant future. Historically, even those natural forms man has found ready made and most to his liking he has seen fit to recondition even more to suit his desires. On contemplating time and monetary value spent on collecting and culturing plants which ten years ago were labeled as discards or useless, one wonders on passing a discredited wayside weed how soon it too will emerge as a highly respected member of the chosen or its genes will circulate with those of the supposedly best.

Triple hybrids and bridge crosses have been found useful in bringing together the chromosomes of two highly incompatible species, the third species serving as the intermediary. One such triple cereal hybrid includes the chromosome sets of three genera. One purpose of such crosses is to introduce into a favorable agronomic race some desirable character, as hardiness, drought resistance or disease immunity.

Aneuploidy also occurs in natural species. Among cereals some races of common rye almost habitually attain an extra chromosome or one or more fragments of chromosomes. The aneuploidy may disappear only to reappear in later generations. Several theories have been proposed as to the basic cause of this easily detected form of chromosome instability apparently inherent in races of rye.

Aneuploidy frequently follows in the wake of other chromosome aberrations, numerical or structural. The loss or gain of a chromosome or two may express itself phenotypically, as in some speltoids, compactoids and fatuoids.

No less profound than numerical changes and morphologically evident structural changes as to eventual results are the internal chromosome reconstructions, large and small. Some of these internal alterations are detected with more or less difficulty by observing the form of the meiotic pairing. The interpretations to be placed on the pairing procedures demand considerable cytological and genetical familiarity with the material studied before fairly accurate conclusions may be offered. Many modifying influences may affect pairing, some of which may be external, as temperature, others internal, as genic control.

Advisably more attention is being extended to the reproductive morphology of cereals and other grasses. These studies should prove fruitful in discovering more of the basic causes of various types of sterility, including failures of hybrid embryos, and the effects of the intricate nuclear interactions among embryo, endosperm and ovular tissues in hybrids between parents of like as well as unlike chromosome numbers.

Little progress may seem to have been made during the past ten years in the unravelling of cereal phylogeny. Yet the reporting of discoveries of new natural species and the synthesis of 42-chromosome wheats similar to the vulgare and spelt types are definitely forward steps.

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